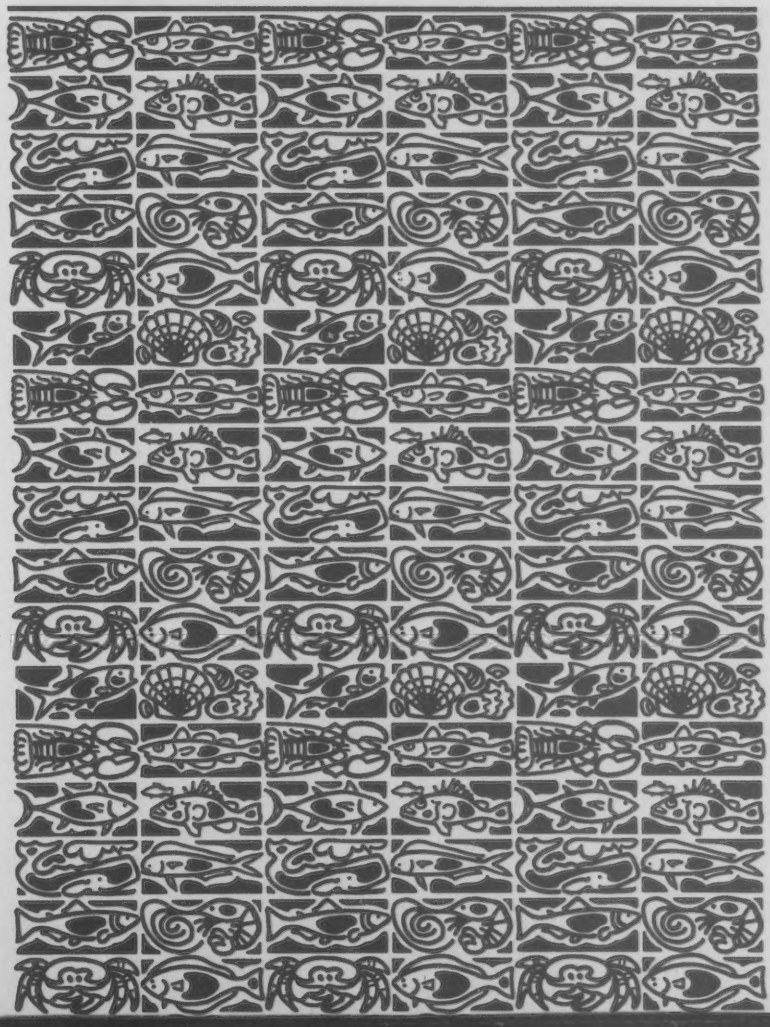
U.S. Department
of Commerce

Volume 92
Number 3
July 1994

Fishery Bulletin



U.S. Department of Commerce
Ronald H. Brown
Secretary

National Oceanic and Atmospheric Administration
D. James Baker
Under Secretary for
Oceans and Atmosphere

National Marine Fisheries Service
Rolland A. Schmitten
Assistant Administrator
for Fisheries

Fishery Bulletin

Scientific Editor
Dr. Ronald W. Hardy
Northwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, Washington 98112-2097

Editorial Committee
Dr. Andrew E. Dizon National Marine Fisheries Service
Dr. Linda L. Jones National Marine Fisheries Service
Dr. Richard D. Methot National Marine Fisheries Service
Dr. Theodore W. Pietsch University of Washington
Dr. Joseph E. Powers National Marine Fisheries Service
Dr. Tim D. Smith National Marine Fisheries Service

Managing Editor
Sharyn Matriotti
National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Second class postage is paid in Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, Attn: Chief, Mail List Branch, Mail Stop SSOM, Washington, DC 20402-9373.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $27.00 domestic and $33.75 foreign. Cost per single issue: $13.00 domestic and $16.25 foreign. **See back page for order form.**

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department of Commerce
Seattle, Washington

Volume 92
Number 3
July 1994

Fishery Bulletin

Contents

iii **Errata**

Articles

481 **Castillo, Gonzalo C., Hiram W. Li, and James T. Golden**
Environmentally induced recruitment variation in petrale sole, *Eopsetta jordani*

494 **Creaser, Edwin P., and Herbert C. Perkins**
The distribution, food, and age of juvenile bluefish, *Pomatomus saltatrix*, in Maine

509 **David, Andrew W., J. Jeffery Isley, and Churchill B. Grimes**
Differences between the sagitta, lapillus, and asteriscus in estimating age and growth in juvenile red drum, *Sciaenops ocellatus*

516 **Dee, Anderson J., and James D. Parrish**
Reproductive and tropic ecology of the soldierfish *Myripristis amaena* in tropical fisheries

531 **Di Giácomo, Edgardo E., and Maria Raquel Perier**
Reproductive biology of the cockfish, *Callorhynchus callorhynchus* (Holocephali: Callorhynchidae), in Patagonian waters (Argentina)

540 **Kendall, Arthur W., Jr., Lewis S. Incze, Peter B. Ortner, Shailer R. Cummings, and Patricia K. Brown**
The vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska

555 **Lowerre-Barbieri, Susan K., Mark E. Chittenden Jr., and Cynthia M. Jones**
A comparison of a validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional scale method

569 **McKinnon, Jeff**
Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus,* in the coastal waters of central Peru

579 **Müter, Franz-Josef, and Brenda L. Norcross**
Distribution, abundance, and growth of larval walleye pollock, *Theragra chalcogramma,* in an Alaskan fjord

591 **Norcross, Brenda L., and David M. Wyanski**
Interannual variation in the recruitment pattern and abundance of age-0 summer flounder, *Paralichthys dentatus,* in Virginia estuaries

599 **Sardà, Francisco, Joan E. Cartes, and Walter Norbis**
Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* (Decapoda: Aristeidae) population in the western Mediterranean

608 **Steimle, Frank W., Dorothy Jeffress, Stephen A. Fromm, Robert N. Reid, Joseph J. Vitaliano, and Ann Frame**
Predator-prey relationships of winter flounder, *Pleuronectes americanus,* in the New York Bight apex

620 **Weinberg, Kenneth L.**
Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington

Notes

633 **DeLancey, Lawrence B., James E. Jenkins, and J. David Whitaker**
Results of long-term, seasonal sampling for *Penaeus* postlarvae at Breach Inlet, South Carolina

641 **Forward, Richard B., Jr., William F. Hettler, and Donald E. Hoss**
Swimbladder deflation in the Atlantic menhaden, *Brevoortia tryannus*

647 **Gilman, Sharon L.**
An energy budget for northern sand lance, *Ammodytes dubius,* on Georges Bank, 1977–1986

655 **Stanley, Richard D., Bruce M. Leaman, Lewis Haldorson, and Victoria M. O'Connell**
Movements of tagged adult yellowtail rockfish, *Sebastes flavidus,* off the west coast of North America

664 **Xiao, Yongshun, and David C. Ramm**
A simple generalized model of allometry, with examples of length and weight relationships for 14 species of groundfish

Errata

Thompson, Grant G.
Variations on a simple dynamic pool model
Fish. Bull. 91(4):718–731

Equation 1 should read as follows:

$$w(a) = w_r\left(\frac{a-a_0}{a_r-a_0}\right)$$

Equation 26 should read as follows:

$$B_f(F') = \left(\frac{b(F',a_f)}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right)$$

Appendix Equation A5 should read as follows:

$$BPR(F') = \int_{a_r}^{\infty} w_r\left(\frac{a-a_0}{a_r-a_0}\right)^n e^{-M(1+F')(a-a_r)}da$$

$$= \left(\frac{w_r}{M}\right)\sum_{k=0}^{n}\frac{(n)_k K''^k}{(1+F')^{k+1}}.$$

Volume and page numbers for the following citation should be corrected to read as follows:

Thompson, G. G.
1992. Management advice from a simple dynamic pool model. Fish. Bull. 90:552–560.

The National Marine Fisheries Service (NMFS) does not approve, recommend, or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends, or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

Environmentally induced recruitment variation in petrale sole, *Eopsetta jordani*

Gonzalo C. Castillo
Hiram W. Li
Oregon Cooperative Fishery Research Unit, U.S. Fish and Wildlife Service
Nash Hall 104, Department of Fisheries and Wildlife,
Oregon State University, Corvallis, Oregon 97331

James T. Golden
Hatfield Marine Science Center, Oregon Department of Fish and Wildlife
Building 3, Newport, Oregon 97365.

Abstract.—Potential effects of parental stock size and environmental factors on year-class strength (YCS) of petrale sole, *Eopsetta jordani*, were investigated in two areas off Oregon and Washington (Pacific States Marine Fisheries Commission areas 2B: 42°50'N–44°18'N, and 3A: 45°46'N–47°20'N). Parental egg production indices and YCS were not consistently correlated over the period 1970 to 1977. Variation in YCS between 1958 and 1977 was associated with oceanographic conditions from winter to early spring, the period in which pelagic larval stages are most abundant. A regression model based on indices of offshore Ekman transport from January to March and alongshore transport from December to February accounted for nearly 55% of the YCS variation in Area 2B. In Area 3A, the previous two indices plus sea surface temperature from December to February explained about 65% of the YCS variation. Inshore advection of eggs and larvae could favor settlement of juveniles into nearshore areas and increase the subsequent recruitment strength of petrale sole.

Manuscript accepted 8 December 1993.
Fishery Bulletin 92:481–493 (1994).

Recruitment fluctuations in fish populations are ascribed to many physicochemical factors and biological processes, including parental stock size and fishing (Ricker, 1975; Shepherd et al., 1984). However, the importance of various factors to the recruitment of most species of fish is virtually unknown. Although year-class strength (YCS) of many fishes is thought to be determined at the egg and larval stages (Sharp[1]; Rothschild and Rooth, 1982), it may also be significantly affected during the postlarval stages (Smith, 1981; Sissenwine, 1984).

Increasing evidence suggests that oceanographic conditions affect the recruitment of many fishes in the Northeast Pacific Ocean (e.g. Parrish et al., 1981; Bailey and Incze, 1985; Hollowed et al., 1987; Botsford et al., 1989). A recent hypothesis suggests that recruitment of groundfish off the west coast of the United States is related to the timing of the spring transition, a period of major changes in oceanographic conditions.[2] On the Oregon–Washington shelf oceanographic conditions exhibit strong seasonal patterns (e.g. Huyer et al., 1975; Halpern, 1976; Huyer, 1977; Landry et al., 1989). In winter, alongshore currents are northward at all depths, and cross-shore surface currents flow inshore resulting in downwelling. In spring, flow is southward at all depths but stronger near the surface. The spring transition usually occurs within a one week period during March or April (Strub et al., 1987; Strub and James, 1988). In summer, a surface coastal current flows southwestward and the attendant offshore transport causes upwelling; however, deep flow is northward. In fall, alongshore currents are northward at all depths.

Petrale sole, *Eopsetta jordani*, Pleuronectidae, is a commercially important flatfish of the northeast Pacific Ocean (Ketchen and Forrester, 1966). It is continuously distributed from the Bering Sea (58°N–152°W) to Baja California (32°26'N–117°16'W) (Roedel, 1953; Hitz and

[1] Sharp, G. D. 1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. *In* Sharp, G. D. (rapporteur), Report and supporting documentation of the workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 15–59. Int. Ocean. Comm. Workshop Rep. 28.

[2] Lynn, R. J. Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038. Personal commun., 1991.

Rathjen, 1965). Recruitment fluctuations of petrale sole appear to be strongly related to environmental factors (Ketchen and Forrester, 1966). Ketchen (1956) demonstrated a positive correlation between winter sea surface temperature and recruitment of petrale sole off British Columbia from the middle 1940's to the middle 1950's. In the same area, Ketchen and Forrester (1966) postulated that warmer sea surface temperatures and onshore transport of pelagic early life stages could favor recruitment of this species.

Two central spawning areas of petrale sole, Heceta Bank and Willapa Deep, are located off Oregon and Washington (Fig. 1). Petrale sole spawn from late fall to early spring at depths of about 300–450 m (Cleaver, 1949; Harry, 1959; DiDonato and Pasquale, 1970; Pedersen, 1975). The incubation period of newly fertilized eggs ranges from about 6 to 13 days (Alderdice and Forrester, 1971). The eggs and yolk-sac larvae are stenohaline and stenothermal (Alderdice and Forrester, 1971). Development of pelagic eggs and larvae occurs mainly from winter to spring, followed by the presettlement and postsettlement juvenile stages from summer to fall respectively (Fig. 2). Although petrale sole larvae have been found from 2 to 120 km offshore, Pearcy et al. (1977) collected nearly 50% of them 83–120 km offshore. However, postsettlement juveniles have only been found at 18–90 m depth in the inner continental shelf (Ketchen and Forrester, 1966; Gregory and Jow, 1976; Pearcy et al., 1977).

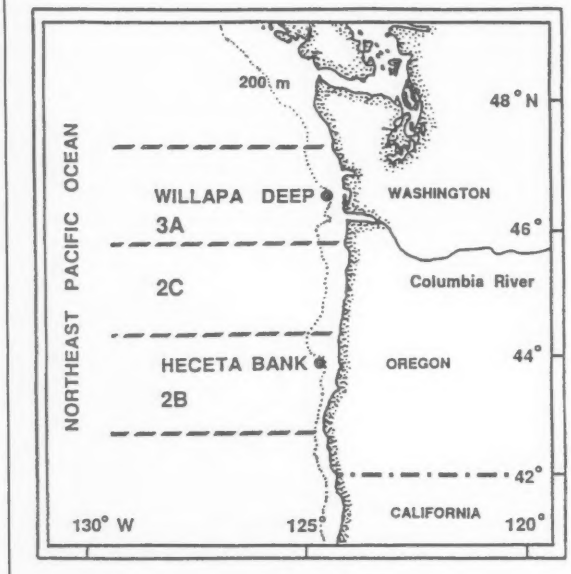


Figure 1

Location of Willapa Deep and Heceta Bank spawning grounds of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 3A and 2B. Spawning areas are located nearly 50 km offshore (modified from Pedersen, 1975).

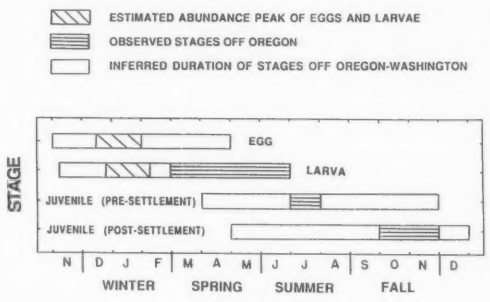


Figure 2

Estimated duration of life stages of petrale sole, *Eopsetta jordani*, off Oregon and Washington from the beginning of the spawning period to the time in which most age-0 juveniles are found settled in the inner continental shelf. The inferred temporal occurrence of life stages was based on the reported duration of spawning, incubation period and presence of presettlement and postsettlement juveniles in the Northeast Pacific Ocean (based on Cleaver, 1949; Harry, 1959; Best, 1963; Porter, 1964; Ketchen and Forrester, 1966; Alderdice and Forrester, 1971; Gregory and Jow, 1976; and Pearcy et al., 1977).

The recruitment patterns of petrale sole off Oregon and Washington demonstrated consecutive series of cohorts alternating between below average (weak) YCS and above average (strong) YCS over the base period 1958–77 (Castillo, 1992). Possible causes for such recruitment variations have not yet been studied. Our objectives were to determine 1) if spawning biomass of petrale sole is correlated with YCS, 2) if YCS fluctuations are associated with selected environmental factors, and 3) the percentage of YCS variation explained by environmental factors.

Data and methods

We selected two locations off Oregon and Washington to investigate the effect of environmental factors on YCS of petrale sole: Pacific States Marine Fisheries Commission[3] areas 2B (42° 50'N–44°18'N) and 3A (45°46'N–47°20'N) (Fig. 1). Indi-

[3] Named Pacific Marine Fisheries Commission (PMFC) areas until 1990.

ces of YCS for petrale sole were obtained from cohort analyses of numbers of females recruited to six years of age in areas 2B and 3A (Table 1). These YCS indices represent the recruitment strength of year classes hatched from 1958 to 1977. Males were excluded from these YCS indices because of problems of increasing age underestimation in fish over 8 years.[4] However, because recruitment variation was similar in males and females of younger age groups, the YCS indices should be representative of both sexes.

Potential egg production was used as a proxy for spawning biomass (e.g. Hayman and Tyler, 1980). Egg production was estimated from fecundity and maturity information (Porter, 1964) and from cohort analyses of the parental stock for years 1970 to 1977 (Castillo, 1992). Annual potential egg production was estimated as the sum of the age-specific products of the numbers of females, their fecundity, and their percent maturity. The number of females was estimated from the observed annual sex ratio in the commercial landings. Females composed on average 58% of petrale sole landed. Egg production was averaged for fish over age 13 years because of the scarcity of older females.

Eight environmental indices available within, or near, areas 2B and 3A were used to investigate possible correlations with petrale sole YCS (Table 2). Ocean transport calculations provided by The Pacific Fisheries Environmental Group (PFEG) were based on Bakun (1973; after Fofonoff[5]). Sverdrup transport was calculated by PFEG by using a finite difference form of equation six in Nelson (1977)[6]. A proxy for salinity was based on observations of water density at constant temperature available at the Columbia River estuary (Table 2, Fig. 1). The timing of the spring transition was obtained from Strub and James

[4] Recent use of the break-and-burn technique for aging otoliths showed that males grow more slowly and lay down less year-marks (annuli) on the surface of the otolith than females (William H. Barss, Oregon Department of Fish and Wildlife, Newport, OR 97365, unpubl. data).

[5] Fofonoff, N. P. 1960. Transport computations for the North Pacific Ocean—1958. Fish. Res. Board Can. Manuscr. Rep. Oceanogr. and Limnol. No. 80.

[6] $M_y = \vec{k}(\nabla \times \vec{\tau})/\beta$ where: M_y is the meridional component of the vertically integrated mass transport, $\vec{k}(\nabla \times \vec{\tau})$ is the vertical component of the wind stress curl, and β is the meridional derivative of the Coriolis parameter.

Table 1

Cohort analyses of numbers of female petrale sole, *Eopsetta jordani*, reaching 6 years of age in Pacific States Marine Fisheries Commission areas 2B and 3A (Castillo, 1992; after Jones, 1981). Both year-class strength indices were significantly correlated with Summed-CPUE indices ($P \leq 0.05$, Castillo, 1992; after Hayman et al., 1980).

Cohort (year)	Year-class strength (thousands of fish)	
	Area 2B	Area 3A
1958	208	543
1959	278	544
1960	309	624
1961	385	692
1962	231	333
1963	296	421
1964	240	365
1965	280	547
1966	487	954
1967	352	703
1968	419	737
1969	349	558
1970	426	651
1971	421	570
1972	373	463
1973	356	415
1974	259	326
1975	193	332
1976	157	286
1977	223	424

Table 2

Environmental indices used in correlations with year-class strength of petrale sole, *Eopsetta jordani*. Recruitment areas include Pacific States Marine Fisheries Commission areas 2B and 3A. (Source of data is indicated for each environmental factor.)

Environmental index	Recruitment area
Sea surface atmospheric pressure[1, 3]	2B, 3A
Alongshore coastal transport indices	
Mean sea level[2]	
Neah Bay (48°22'N–124°38' W)	3A
Crescent City (41°45'N–124°12' W)	2B
Northward Ekman transport[1, 3]	2B, 3A
Northward Sverdrup transport[1, 3]	2B, 3A
Offshore Ekman transport[1, 3]	2B, 3A
Cube of wind speed[1, 3]	2B, 3A
Water properties	
Sea surface temperature[3]	
(43°N–44.9°N), (124°W–124.9°W)	2B
(46°N–47.9°N), (124°W–124.9°W)	3A
Salinity index Columbia River[2]	
Estuary (46°13'N–123°45'W)	2B 3A

[1] Computed at 45° N–125° W.
[2] Tidal Datum Quality Assurance Section, NOAA, Rockville, MD 20852.
[3] Pacific Fisheries Environmental Group, P.O. Box 831, Monterey, CA 93942.

(1988). However, for years not available from Strub and James, it was estimated from weekly upwelling indices (at 45°N 125°W, Bakun, 1975; Mason and Bakun, 1986). In the latter case the time of spring transition was assigned to the first week of the year in which the weekly upwelling index became positive and remained positive for at least another week. The spring transition dates reported by Strub and James (1988) were highly correlated with our estimates (r=0.80; P<0.01). Because March is usually a month of predominant onshore Ekman transport prior to the spring transition (i.e. negative offshore Ekman transport), we determined whether YCS variation was correlated with mean onshore Ekman transport during March.

Analytical methods

Spearman's correlation analyses (Tate and Clelland, 1957) were used to account for linear and nonlinear monotonic associations between YCS and independent variables (i.e. potential egg production, environmental factors, and timing of the spring transition). Independent variables were lagged to the first year of life of each cohort to determine potential influences on YCS at the time year classes were born. Exploratory Spearman's correlation analyses were used for each season of the year because of the seasonality of different early life stages and environmental factors (Fig. 2, Appendix A).

Because many environmental-YCS relationships showed anomalous correlations during the 1958 El Niño, one of the largest El Niño events in the twentieth century (Cannon et al., 1985), this year was not included in Spearman's correlation analyses. However, after the most consistent Spearman's correlations for 1959–77 were established, all years from 1958 to 1977 were considered in regression analyses. Such regressions consisted of estimated YCS on environmental anomalies. These anomalies were computed as the actual seasonal value of a given factor minus its long-term mean for 1958–77. The use of anomalies as independent variables was justified to reduce multicollinearity effects in polynomial regressions (Neter et al., 1989).

The Bonferroni correction and the P-value plot of Schweder and Spjotvoll (1982) required individual P-values ≈0.001 for an overall P-value = 0.05 in multiple comparisons between YCS and environmental factors. Since such P-values would have made it difficult to detect meaningful ecological relationships, significance of correlations was based on individual P-values ≤0.05. Although statistical significance in our study was based on nonfiltered data (here after referred to as original series), unrelated trends in original series often cause spurious correlations and conceal the extent of year-to-year associations (Dickey et al., 1986; Norton[7]; Cohen et al., 1991). Therefore, first-order differencing was used to evaluate the reliability of correlations based on the original series (Chatfield, 1989; here after referred to as filtered series). By this criterion, a significant correlation for original series was deemed reliable only if the attendant correlation for the filtered series had the same correlation sign and a minimum absolute value ($|r| > 0.10$). Although this procedure does not account for P-values of filtered series, it provides a more consistent selection of factors potentially associated with recruitment variation.

Results

Potential spawning biomass

The effect of spawning biomass on subsequent recruitment strength was minimal as indicated by similar variations from 1970 to 1977 in YCS per parental egg and the YCS index (Fig. 3). The initial decline in YCS in the 1970's was not linked to a de-

[7] Norton, J. 1990. Relationship between California Current temperatures and intensity of the Aleutian Low. Southwest Fisheries Science Center. Report of activities. March–April 1990. La Jolla, CA, p. 16–18.

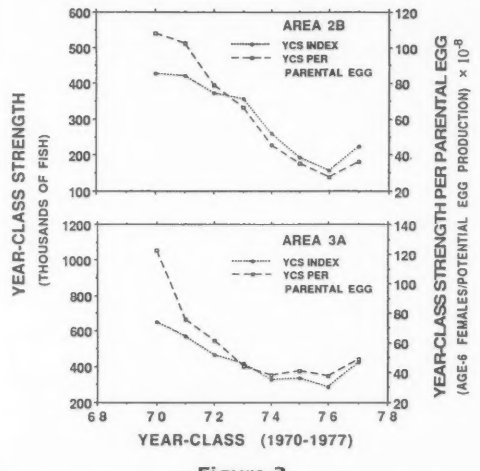


Figure 3

Comparison between year-class strength indices of petrale sole, *Eopsetta jordani*, with the attendant number of fish reaching age 6 per parental egg in Pacific States Marine Fisheries Commission areas 2B and 3A. (Cohorts considered in year-class strength indices were hatched between 1970 and 1977.)

crease in parental-stock size, as negative trends between YCS and potential egg production were observed for year classes from 1970 to 1977 (Area 2B: r=–0.81, P<0.05; Area 3A: r=–0.57, P<0.20; Fig. 4A). Examination of the attendant filtered series did not support a density-dependent relationship when the size of the parental stock was large (e.g. Ricker, 1954; Area 2B: r=0.21, Area 3A: r=0.07; Fig. 4B).

Environmental-YCS fluctuations (1959–1977)

Alongshore transport indices

1 Mean sea level height The strongest northward and southward coastal flow generally coincide with the highest and lowest mean sea levels off Oregon (Huyer et al., 1975). Long-term seasonal sea levels indicated that stronger northward and southward flows from 1959 to 1977 occurred in winter and summer, respectively (Appendix A). Correlations between YCS and mean sea level were highest in winter for both study areas (Fig. 5A). The attendant filtered series showed lower but consistent correlations for winter (Fig. 6A). Thus, recruitment strength of petrale sole seems to be associated with interannual variation in nearshore northward transport during winter.

2 Northward Ekman transport This index indicates the alongshore flow of surface mixed layers driven by wind stress. Unlike sea level height, there was no correlation between northward Ekman transport and YCS (Figs. 5B and 6B). The four long-term seasonal means of this index indicated predominantly negative northward transport (i.e. southward transport) of surface waters at offshore areas (45°N–125°W, Appendix A).

3 Northward Sverdrup transport This index measures alongshore transport over the entire water column by adding geostrophic flow to Ekman transport. For nonwinter seasons, the long-term seasonal means of this index showed southward transport of offshore waters (45°N–125°W, Appendix A). Northward Sverdrup transport and YCS were not consistently correlated (Figs. 5C and 6C).

Offshore Ekman transport The long-term seasonal means of this index indicated average offshore transport of surface waters and upwelling from spring to summer followed by onshore transport and downwelling from fall to winter (Appendix A). Winter offshore Ekman transport and YCS showed clear and consistent negative correlations in both study areas (Figs. 5D and 6D).

Cube of wind speed This index reflects the turbulence transferred to the sea surface by the wind (Niiler and Kraus, 1977). Although cube of wind speed was correlated with YCS for winter and spring (Figs. 5E and 6E), these correlations were largely explained by onshore Ekman transport during this period. Moreover, correlations for spring vanished in both areas when March was excluded from the analyses. Thus, cube of wind speed seems to be spuriously correlated with YCS.

Sea surface temperature Long-term seasonal means of sea surface temperature increased from winter through summer and decreased from fall through winter (Appendix A). Correlations between YCS and sea surface temperatures for winter and spring showed high positive

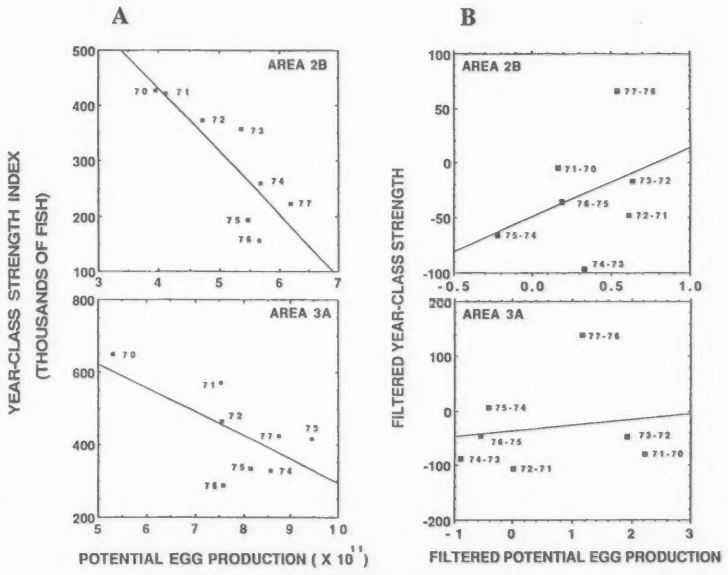


Figure 4

Variation of year-class strength of petrale sole, *Eopsetta jordani*, in relation to potential parental egg production in Pacific States Marine Fisheries Commission areas 2B and 3A. Comparison is shown for (**A**) original and (**B**) filtered series. Cohorts hatched between 1970 and 1977 (years are identified by the last two digits).

values only in Area 3A, particularly during winter (Figs. 5F and 6F). Therefore, warmer temperatures may result in increased survival of eggs and/or larvae of petrale sole in Area 3A.

Nearshore salinity index This index reflects nearshore salinity variations caused by the Columbia River plume. Although high correlations between filtered YCS and the salinity index were detected for winter and summer, no significant correlations were observed for original series (Figs. 5G and 6G).

Sea surface atmospheric pressure Nearshore transport and water properties such as temperature, salinity and density are greatly influenced by the North

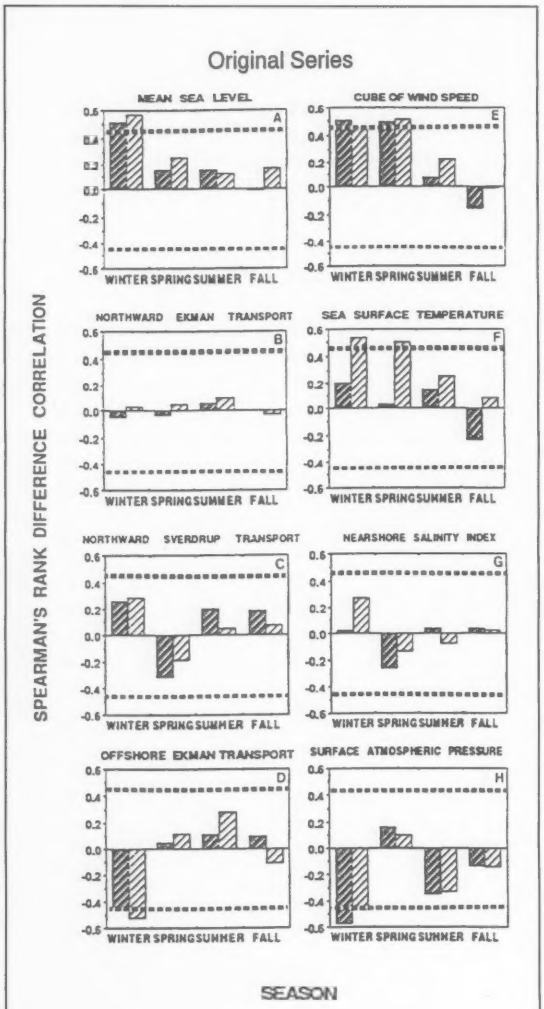


Figure 5

Spearman's correlations between year-class strength indices of petrale sole, *Eopsetta jordani*, and seasonal averages of environmental factors lagged to the first year of life (Table 2). Correlation for cohorts 1959 to 1977 are compared for Pacific States Marine Fisheries Commission areas 2B (dark bar) and 3A (light bar). Dashed lines correspond to $P = 0.05$ for individual correlations.

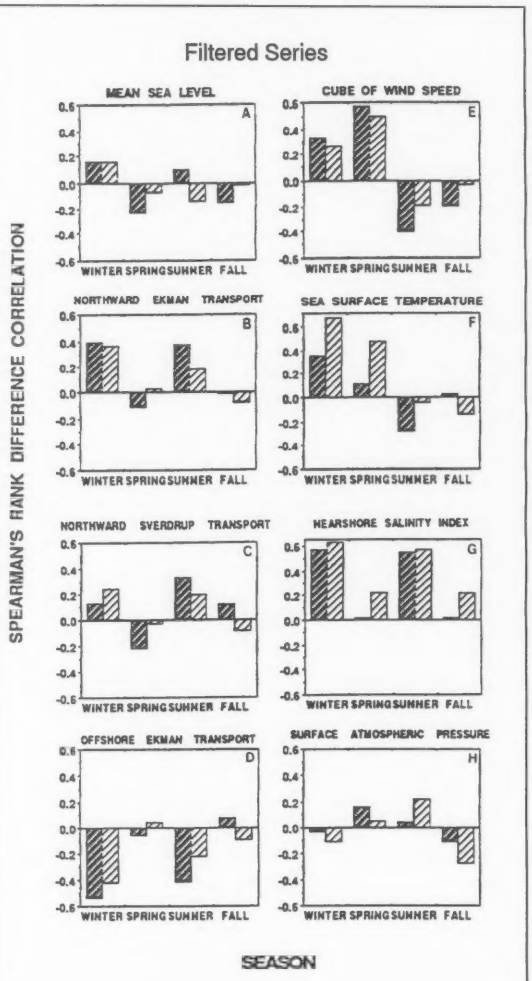


Figure 6

Spearman's correlations between filtered year-class strength indices of petrale sole, *Eopsetta jordani*, and filtered seasonal averages of environmental factors lagged to the first year of life for cohorts from 1959 to 1977 (Table 2). Areas compared are Pacific States Marine Fisheries Commission 2B (dark bar) and 3A (light bar). Significance of correlations was based on original series (see analytical methods).

Pacific high and Aleutian low pressure systems (Huyer, 1983). Large negative correlations between YCS and winter sea surface atmospheric pressure were evident in both areas (Fig. 5H). However, filtered series suggested that this index was spuriously correlated with recruitment strength (Fig. 6H).

Effects of the spring transition on YCS Correlations between YCS and the week of the spring transition from 1967 to 1977 were not significant (Area 2B: r=0.27, Area 3A: r=0.22; P>0.20; Fig. 7A). Moreover, correlations for attendant filtered series were negative (Area 2B: r=–0.18, Area 3A: r=–0.32; Fig. 7B). However, onshore transport during early spring can affect YCS as recruitment strength was correlated with mean onshore Ekman transport during March in both study areas (Area 2B: r=0.55, Area 3A: r=0.50; P<0.05). Such correlations were also supported by the attendant filtered series (Area 2B: r=0.58, Area 3B: r=0.42).

Environmental-YCS series Based on exploratory correlation analyses for original and filtered series, winter offshore Ekman transport seemed to be the main factor affecting YCS of petrale sole in areas 2B and 3A. In subsequent analyses, the period January–March was chosen for describing the association between YCS and offshore/onshore Ekman transport. This period was selected because of the importance of onshore transport on YCS during March. Moreover, correlations between offshore Ekman transport and YCS tended to be higher during January–March (original and filtered series respectively: Area 2B, r=–0.48 and –0.67; Area 3A: r=–0.52 and –0.65; P<0.05) than December–February (original and filtered series respectively: Area 2B, r=–0.46 and –0.53; Area 3A: r=–0.52 and –0.42; P≤0.05).

Comparing onshore Ekman transport with YCS, we found that two periods of reduced onshore Ekman transport (1962–65 and 1974–77) coincided with weak year classes of petrale sole (Fig. 8). The years 1958, 1961, and 1968 showed the largest positive anomalies in onshore Ekman transport from 1958 to 1977. However, unlike 1961 and 1968, the 1958 El Niño produced weak YCS in Area 2B and near-average YCS in Area 3A. Other anomalies for indices such as winter and spring sea surface temperature and winter sea level height showed some correspondence with YCS anomalies in Area 3A. In Area 2B, only onshore Ekman transport and sea level height suggested some association with YCS (Figs. 8 and 9).

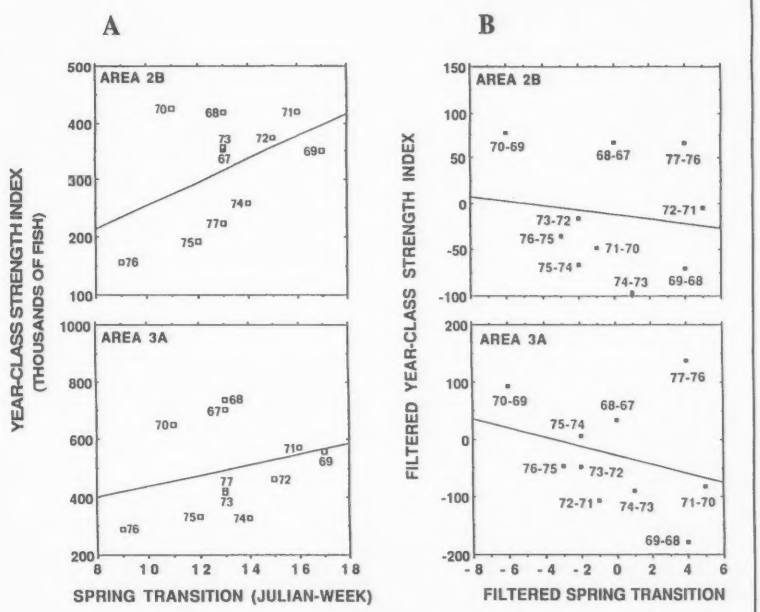


Figure 7

Variation of year-class strength for petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A in relation to the week of the year in which the spring transition occurred. Comparison is shown for (**A**) original and (**B**) filtered series. Year classes are considered hatched between 1967 and 1977 and are identified by the last two digits.

Percentage of YCS variation explained by environmental factors The relationship between YCS and January–March offshore Ekman transport anomalies was best described by second-order polynomial regressions (Fig. 10, Table 3). Associations between YCS and winter sea level height anomalies in areas 2B and 3A, were also described by second-order polynomials (Fig. 11, Table 3). Although the association between YCS and winter sea surface temperature in Area 3A was better described by a second-order polynomial than by a linear regression, only the latter was significant (Fig. 12, Table 3). Except for the year 1958, and for the years with large anomalies in offshore Ekman transport

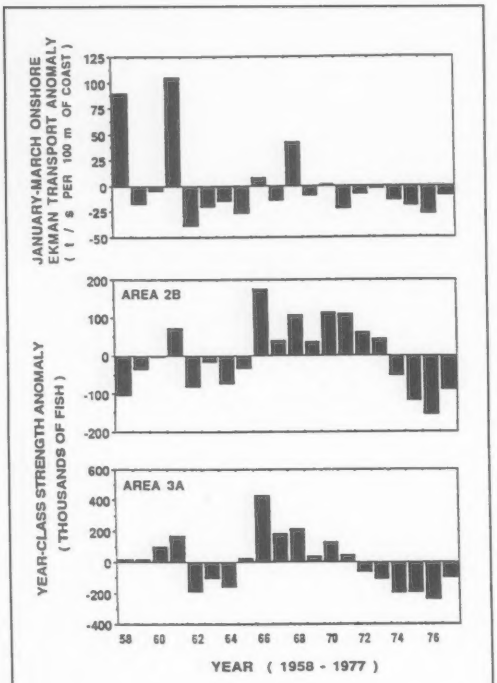

JANUARY-MARCH ONSHORE EKMAN TRANSPORT ANOMALY (1 / s PER 100 m OF COAST)
YEAR-CLASS STRENGTH ANOMALY (THOUSANDS OF FISH)
AREA 2B
AREA 3A
YEAR (1958 - 1977)

Figure 8

Anomalies for mean onshore Ekman transport off Oregon (January to March), and for year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A. (Values computed from the long-term mean 1958–77.)

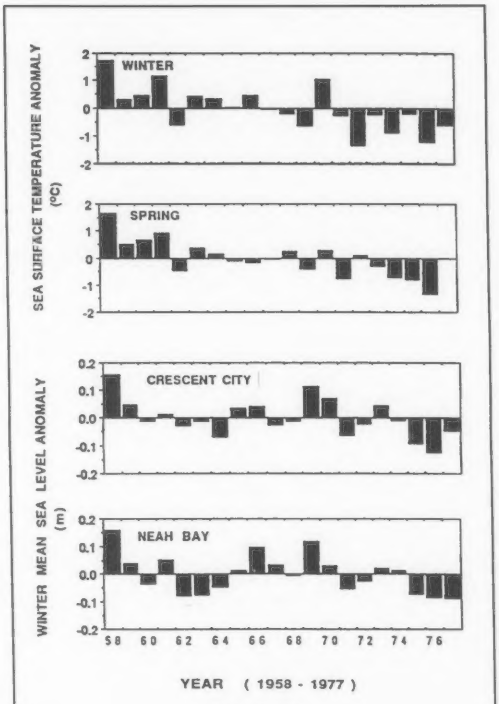


Figure 9

Anomalies of sea level height (Crescent City and Neah Bay), and winter and spring sea surface temperature off Oregon-Washington (considered for Area 3A). Values based on the long-term mean 1958–77. (Locations for environmental indices are shown in Table 2.)

(i.e. 1961, 1968; Fig. 10) and sea level height (i.e. 1969; Fig. 11), a common feature in these regressions is the nearly linear association for most of the studied period.

Regressions for individual environmental factors explained less than 40% of the YCS variation in each area from 1958 to 1977 (Table 3). However, a regression model including offshore Ekman transport and sea level height accounted for nearly 55% of the YCS in Area 2B (Fig. 13). Over the same period in Area 3A, these two environmental factors plus sea surface temperature explained about 65% of the variation in YCS.

Discussion

Recruitment variation of petrale sole in areas 2B and 3A was correlated with oceanographic conditions from winter to early spring, the period in which egg and larval stages of this species are most abundant. Since postsettlement, age-0 petrale sole have only been found within the inner continental shelf (Ketchen and Forrester, 1966; Gregory and Jow, 1976; Pearcy et al., 1977), and YCS and offshore Ekman transport were consistently and negatively correlated, it is possible that inshore advection of eggs and larvae toward nearshore settlement areas may be the major factor determining YCS in this species.

A critical assumption for establishing spawner-recruit relationships is that density-independent survival variation at early life stages is negligible when compared with variation in spawning biomass. This assumption is not consistent with the results obtained in our study, with the lack of spawner-recruit relationships for petrale sole in other areas (Ketchen and Forrester, 1966), and with the results of most flatfish studies (Cushing, 1971; Roff, 1981).

Our findings support the hypothesis that recruitment of petrale sole is dependent on northeastward

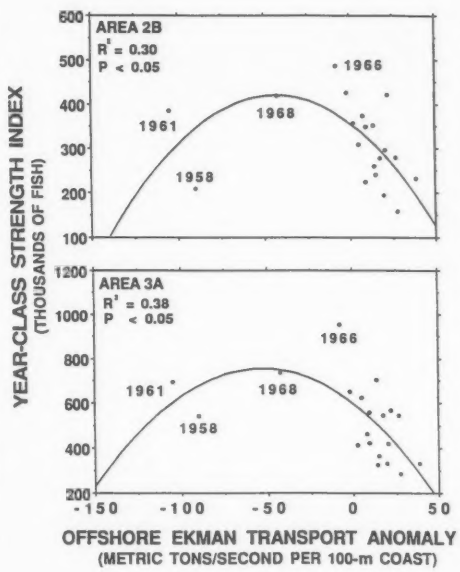


Figure 10

Relations between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A and mean offshore Ekman transport anomaly off Oregon from January to March. (Regression parameters are shown in Table 3.)

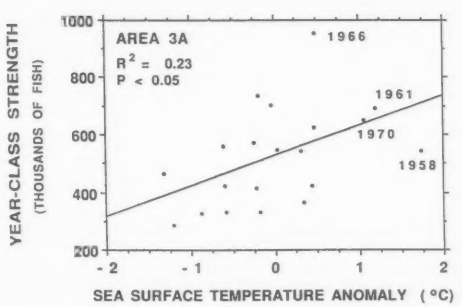


Figure 12

Relation between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission Area 3A and mean winter sea surface temperature anomaly off Oregon-Washington (December-February). (Regression parameters are shown in Table 3.)

transport during winter (Ketchen and Forrester, 1966). The analyses in Area 3A are also consistent with an association between temperature and survival of early life stages of petrale sole (Ketchen and Forrester, 1966; Alderdice and Forrester, 1971). Considering the discharge of the Columbia River into Area 3A and the stenohaline condition of eggs and larvae in this species, possible salinity-YCS associations may be overridden by cross-shore and alongshore advection and sea temperature.

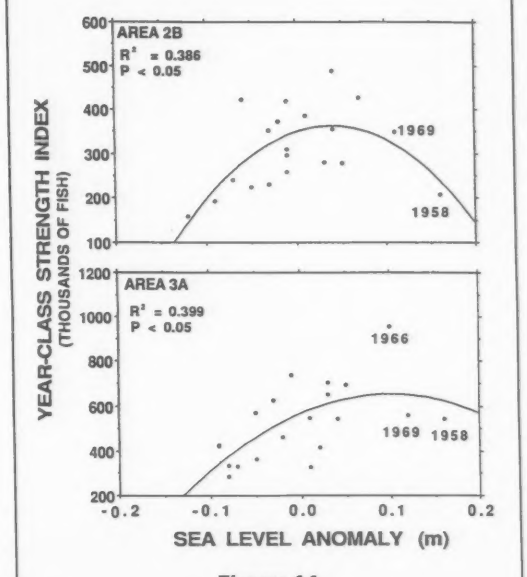


Figure 11

Relations between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A and winter mean sea level height anomalies. (Regression parameters are shown in Table 3.)

Recruitment strength of petrale sole was correlated between areas 2B and 3A (r=0.82, P<0.01). However, the highest determination coefficient for regression models of YCS on environmental factors was obtained in Area 3A. Although the proportion of variation in YCS explained by second-order polynomial regressions was significant for both offshore Ekman transport and sea level height, filtered series suggest that year-to-year variation in YCS were better explained by the former. Unlike Area 3A and off British Columbia (Ketchen and Forrester, 1966), no regression models of YCS on sea surface temperature were significant or marginally significant in Area 2B. The higher positive temperature-YCS association for Area 3A compared with Area 2B is consistent with temperature differences between areas (Appendix A). These observations suggest a latitudinal effect of temperature on the recruitment of petrale sole, that is, higher recruitment toward the poleward range of the

Table 3

Regressions of year-class strength (YCS) for petrale sole, *Eopsetta jordani* (thousands of females attaining age 6), on environmental anomalies in Pacific States Marine Fisheries Commission areas 2B and 3A from 1958 to 1977. Environmental anomalies are based on the long-term mean 1958–77. SST = sea surface temperature anomaly (Dec.–Feb.), SL = mean sea level height anomaly (Dec.–Feb.), Me = offshore Ekman transport anomaly (Jan.–Mar.). $P \leq 0.05$ for significant correlations (n = 20 years). In the last regression model, $R^2 = 0.667$ between predicted YCS ($e^{\ln(YCS)}$) and YCS index ($P<0.05$).

Area	Regression model	R^2	P
	YCS on SST		
3A	$YCS = 524.5048 + 104.8226\ SST$	0.231	<0.05
	YCS on SST and SST²		
3A	$YCS = 550.4459 + 116.8338\ SST - 44.9699\ SST^2$	0.270	0.06*
	YCS on Me and Me²		
2B	$YCS = 357.0224 - 2.9121\ Me - 0.0340\ Me^2$	0.302	<0.05
3A	$YCS = 576.0152 - 4.3035\ Me - 0.0391\ Me^2$	0.381	<0.05
	YCS on SL and SL²		
2B	$YCS = 347.0157 + 625.3314\ SL - 8103.1487\ SL^2$	0.386	<0.05
3A	$YCS = 565.1595 + 1686.4019\ SL - 8512.4524\ SL^2$	0.399	<0.05
	YCS on Me, Me², SL and SL²		
2B	$YCS = 377.9325 - 2.3712\ Me - 0.0255\ Me^2 + 346.4281\ SL - 7477.8599\ SL^2$	0.549	<0.05
3A	$YCS = 608.3490 - 3.8546\ Me - 0.0378\ Me^2 + 1104.2691\ SL - 7115.5843\ SL^2$	0.508	<0.05
	Ln (YCS) on Me, Me², SL, SL², SST and SST²		
3A	$Ln(YCS) = 6.4115 - 0.0068\ Me - 6\times10{-}5\ Me^2 + 1.9585\ SL - 9.0066\ SL^2 + 0.1069\ SST - 0.1321\ SST^2$	0.648	<0.05

* Nonsignificant.

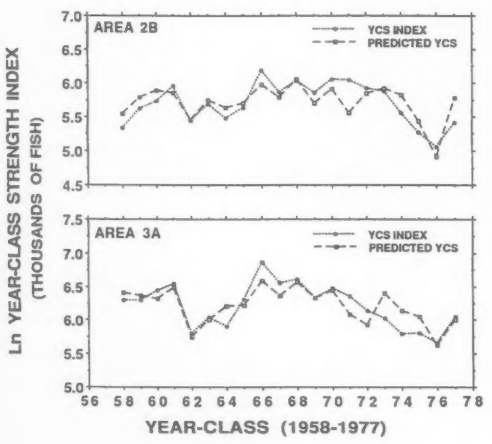


Figure 13

Log-transformed estimated and predicted year-class strength for petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A. Area 2B: prediction is based on anomalies of offshore Ekman transport and sea level height and their attendant squared values. Area 3A: predicted values are based on anomalies of offshore Ekman transport, sea level height, sea surface temperature, and their attendant squared values. (Regression parameters are shown in Table 3.)

species' distribution in warmer years (Cushing, 1982; Bailey and Incze, 1985; Frank, 1991).

The interrelation among oceanographic factors (e.g. Huyer, 1977; Kruse and Huyer, 1983) makes it difficult to determine the importance of any single environmental factor to YCS variation. Hence, the more consistent negative correlation between YCS and offshore Ekman transport in Area 3A than in Area 2B could be due in part to a higher correlation between YCS and sea surface temperature in Area 3A.

Primary production and usable solar radiation seem to be positively correlated during winter and spring off Oregon (Small et al., 1972). However, no associations between YCS of petrale sole and mean usable radiation were observed from solar radiation estimates for winter or spring near areas 2B[8] and 3A[9] (Castillo, unpubl. data). On the other hand, although a nearly tenfold increase in zooplankton production from winter to summer may be stimulated by coastal upwelling off Oregon (Peterson and Miller, 1977), correlations between YCS of petrale sole and spring or summer upwelling indices did not suggest that recruitment strength is primarily controlled by

[8] U.S. Weather Bureau. 1961–1964. Local climatological data, Medford, Municipal Airport, Oregon, U.S. Dep. Commerce. USCOMM-WB-Asheville.

[9] U.S. Weather Bureau. 1958–1964. Local climatological data, Clatsop County Airport, Astoria, Oregon, U.S. Dep. Commerce. USCOMM-WB-Asheville.

zooplankton production. Such inference is consistent with observations for two other species of flatfish in Area 3A (Hayman and Tyler, 1980).

Years of strong cohorts of petrale sole and other flatfishes tended to co-occur off Oregon during the 1960's (e.g. 1961, 1966, and 1968).[10] Year class 1961 was strong for nearly 85% of 13 groundfish species from the Northeast Pacific (Hollowed et al., 1987). The high onshore Ekman transport in winter 1961 (Fig. 10) suggests that major factors controlling YCS in petrale sole are the same for other groundfish species.

Acknowledgments

David Husby (PFEG) provided most of the environmental data. William Pearcy (Oregon State University), Robert Hannah (Oregon Department of Fish and Wildlife), and two anonymous reviewers provided useful suggestions. The research was supported by the Fred Anderson Award, the Department of Fisheries and Wildlife at Oregon State University, the Oregon Cooperative Fishery Research Unit, and the Oregon Department of Fish and Wildlife.

Literature Cited

Alderdice, D. F., and C. R. Forrester.
1971. Effects of salinity and temperature on embryonic development of the petrale sole (*Eopsetta jordani*). J. Fish. Res. Board Can. 28:727–744.

Bailey, K. M., and L. S. Incze.
1985. El Niño and the early life history and recruitment of fishes in temperate marine waters. *In* W. S. Wooster and D. L. Fluharty (eds.), El Niño North, p. 143–165. Wash. Sea Grant Progr. Univ. Wash., Seattle.

Bakun, A.
1973. Coastal upwelling indices, west coast of North America, 1946–71. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.
1975. Daily and weekly upwelling indices, west coast of North America. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.

Best, E. A.
1963. Movements of petrale sole, *Eopsetta jordani* (Lockington) tagged off California. Pac. Mar. Fish. Comm. Bull. 6:24–38.

Botsford, L. W., D. A. Armstrong, and J. M. Shenker.
1989. Oceanographic influences on the dynamics of commercially exploited populations. *In* M. R. Landry and B. M. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 511–563. Elsevier Oceanogr. Ser. 47.

Cannon, G. A., R. K. Reed, and P. E. Pullen.
1985. Comparison of El Niño events off the Pacific Northwest. *In* W. S. Wooster and D. L. Fluharty (eds.), El Niño north, p. 75–84. Wash. Sea Grant Progr. Univ. Wash., Seattle.

Castillo, G. C.
1992. Fluctuations of year-class strength in petrale sole (*Eopsetta jordani*) and their relation to environmental factors. M.S. thesis, Oregon State Univ. Corvallis, OR, 99 p.

Chatfield, C.
1989. The analysis of time series, 4th ed. Chapman and Hall, G.B., 241 p.

Cleaver, F. C.
1949. The Washington otter trawl fishery with reference to the petrale sole (*Eopsetta jordani*). Wash. Dep. Fish., Biol. Rep. 49A:1–45.

Cohen, E. B., D. G. Mountain, and R. O'Boyle.
1991. Local-scale versus large-scale factors affecting recruitment. Can. J. Fish. Aquat. Sci. 48: 1003–1006.

Cushing, D. H.
1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer 33:340–362.
1982. Climate and fisheries. Academic Press, London, 373 p.

Dickey, D. A., W. R. Bell, and R. B. Miller.
1986. Unit roots in time series models: tests and implications. Am. Stat. 40:12–26.

DiDonato, G. S., and N. Pasquale.
1970. Migration of petrale sole tagged in deep water off the Washington coast. Wash. Dep. Fish. Res. Pap. 3:53–61.

Frank, K. T.
1991. Predicting recruitment variation from year-class specific vertebral counts: an analysis of the potential and a plan for verification. Can. J. Fish. Aquat. Sci. 48:1350-1357.

Gregory, P. A., and T. Jow.
1976. The validity of otoliths as indicators of age of petrale sole from California. Calif. Fish Game 62:132–140.

Halpern, D.
1976. Structure of a coastal upwelling event observed off Oregon during July 1973. Deep-Sea Res. 23:495–508.

Harry, G. Y.
1959. Time of spawning, length at maturity, and fecundity of the English, petrale and Dover soles (*Parophrys vetulus*, *Eopsetta jordani*, and *Microstomus pacificus*, respectively). Oreg. Fish Comm. Res. Briefs 7:5–13.

Hayman, R. A., and A. V. Tyler.
1980. Environmental and cohort strength of Dover sole and English sole. Trans. Am. Fish. Soc. 109:54–70.

[10] Demory, R. L., M. J. Hosie, N. T. Eyck, and B. O. Forsberg. 1976. Groundfish surveys on the continental shelf off Oregon, 1971–74. Oregon Department of Fish and Wildlife Information Rep. 76-9.

Hayman, R. A., A. V. Tyler, and R. L. Demory.
1980. A comparison of cohort analysis and catch per unit effort for Dover sole and English sole. Trans. Am. Fish. Soc. 109:35–53.

Hitz, C. R., and W. F. Rathjen.
1965. Bottom trawling surveys of the northeastern Gulf of Alaska. Commer. Fish. Review 27:1–15.

Hollowed, A. B., K. M. Bailey, and W. S. Wooster.
1987. Patterns of recruitment of marine fishes in the Northeast Pacific Ocean. Biol. Oceanogr. 5:99–131.

Huyer, A.
1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnol. Oceanogr. 22:442–453.
1983. Coastal upwelling in the California Current System. Progr. Oceanogr. 12:259–284.

Huyer, A., R. D. Pillsbury, and R. L. Smith.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90–95.

Jones, R.
1981. Analysis of age composition data. *In* The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis), p. 1–17. FAO Fish. Circ. 734.

Ketchen, K. S.
1956. Climatic trends and fluctuations in yield of marine fisheries of the Northeast Pacific. J. Fish. Res. Board Can. 13:357–374.

Ketchen, K. S., and C. R. Forrester.
1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in waters off western Canada. Fish. Res. Board Can. Bull. 153, 195 p.

Kruse, G. H., and A. Huyer.
1983. Relationships among shelf temperatures, coastal sea level, and the coastal upwelling index off Newport, Oregon. Can. J. Fish. Aquat. Sci. 40:238–242.

Landry, M. R., J. R. Postel, W. K. Peterson, and J. Newman.
1989. Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. *In* M. R. Landry and B. M. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 1–40. Elsevier Oceanogr. Ser. 47.

Mason, J. E., and A. Bakun.
1986. Upwelling index update, U.S. west coast, 33°N–48°N latitude. NOAA-TM-NMFS-SWFC-67, 81 p.

Nelson, C. S.
1977. Wind stress and wind stress curl over the California Current. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-714, 87 p.

Neter, J., W. Wasserman, and M. H. Kutner.
1989. Applied linear regression models, 2nd ed. Donneley & Sons Co., 667 p.

Niiler, P. P., and E. B. Kraus.
1977. One-dimensional models in the upper ocean. *In* E. B. Kraus (ed.), Modelling and prediction of the upper layers of the ocean, p. 143–172. Pergamon Press, England.

Parrish, R. H., C. S. Nelson, and A. Bakun.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Pearcy, W. G., M. J. Hosie, and S. L. Richardson.
1977. Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and petrale sole, *Eopsetta jordani*, in waters off Oregon. Fish. Bull. 75:173–183.

Pedersen, M. G.
1975. Movements and growth of petrale sole (*Eopsetta jordani*) tagged off Washington and southern Vancouver Island. J. Fish. Res. Board Can. 32:2169–2177.

Peterson, W. T., and C. B. Miller.
1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fish. Bull. 75:717–724.

Porter, P.
1964. Notes on fecundity, spawning and early life history of petrale sole (*Eopsetta jordani*), with descriptions of flatfish larvae collected in the Pacific Ocean off Humboldt Bay, California. M.S. thesis, Humboldt State College, 98 p.

Ricker, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559–623.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Roedel, P. M.
1953. Common ocean fishes of the California coast. Calif. Dep. Fish Game, Fish Bull. 91, 184 p.

Roff, D. K.
1981. Reproductive uncertainty and the evolution of iteroparity: Why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38:968–977.

Rothschild, B. J., and C. G. Rooth.
1982. Fish ecology III. A foundation for REX, a recruitment experiment. Univ. Miami. Tech. Rep. 82008, 388 p.

Schweder, T., and E. Spjotvoll.
1982. Plots of *P*-values to evaluate many tests simultaneously. Biometrika 69:493–502.

Shepherd, J. G., J. G. Pope, and R. D. Cousens.
1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Reun. Cons. int. Explor. Mer 185:255–267.

Sissenwine, M. P.
1984. Why do fish populations vary? *In* R. M. May (ed.), Exploitation of marine communities, p. 59–94. Springer-Verlag, Berlin.

Small, L. F., H. Curl, and W. A. Glooschenko.
1972. Effects of solar radiation and upwelling on daily primary production off Oregon. J. Fish. Res. Board Can. 29:1269–1275.

Smith, P. E.
1981. Time series of anchovy larva and juvenile abundance. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:201.

Strub, P. T., and C. James.
1988. Atmospheric conditions during the spring and fall transitions in the coastal ocean off western United States. J. Geophys. Res. 93: 15561–15584.

Strub, P. T., J. S. Allen, A. Huyer, and R. L. Smith.
1987. Large-scale structure of the spring transition in the coastal ocean off western North America. J. Geophys. Res. 92:1527–1544.

Tate, M. W., and R. C. Clelland.
1957. Nonparametric and shortcut statistics in the social, biological and medical sciences. Interstate Printers and Publishers, Inc., Danville, IL, 171 p.

Appendix A

Long-term seasonal means (1959–77) of environmental indices used in exploratory correlation analyses. Except for mean sea level height and sea surface temperature, only one index per environmental factor was considered for Pacific States Marine Fisheries Commission areas 2B and 3A. (Geographical locations and sources for environmental indices are shown in Table 2.)

	Environmental indices									
	Mean sea level height[1]		Northward Ekman tran.[2]	Northward Sverdrup tran.[3]	Offshore Ekman tran.[4]	Cube of wind speed[5]	Sea surface temperature[6]		Nearshore salinity index[7]	Sea surface atmos. pressure[8]
Season	Area 2B	Area 3A					Area 2B	Area 3A		
Winter	2.09	2.33	– 26.09	18.43	– 72.31	155.16	10.40	9.38	9984.63	1017.60
Spring	1.93	2.19	– 20.02	– 117.43	9.97	46.17	10.73	10.16	9990.12	1018.65
Summer	1.88	2.25	– 14.24	– 200.35	61.28	104.99	13.67	13.85	10102.03	1018.58
Fall	1.98	2.29	– 10.69	– 15.63	– 19.71	53.31	13.22	12.87	9999.48	1017.17

[1] Meters.
[2] Value × 10 = metric tons per second per kilometer.
[3] Value × 100 = metric tons per second per kilometer.
[4] Metric tons per second per 100 meter of coast width.
[5] (meters/second)^3.
[6] Value = Celsius degrees.
[7] Value/10,000=water density (grams/cm^3) at 15°C.
[8] Millibars.

The distribution, food, and age of juvenile bluefish, *Pomatomus saltatrix*, in Maine

Edwin P. Creaser
Herbert C. Perkins
Fisheries Research Laboratory, Department of Marine Resources
West Boothbay Harbor, Maine 04575

Abstract.—The bluefish, *Pomatomus saltatrix* (Linnaeus), is abundant in the South and Middle Atlantic Bights, where more than 75% of the shore-based catches are juveniles (age 0). No information is available on the distribution, food, and age of juvenile bluefish north of the Middle Atlantic Bight. The objectives of the present study were to review and summarize unpublished records of catch locations, to characterize the diet of juvenile bluefish, and to derive parent spawning dates (and possible spawning locations) for juvenile bluefish in Maine. Most observations of juvenile bluefish were from southwestern Maine. The most northeasterly site was Little Kennebec Bay (near Machiasport, Maine). During this study, juvenile bluefish were collected from three locations: Marsh River (1990–1991), Sagadahoc Bay (1990), and Merepoint Bay (1991). The diet of juvenile bluefish varied with size. Fish from Sagadahoc Bay, measuring 37–64 mm fork length (FL), fed predominantly on mysids and copepods. Fish from the Marsh River, measuring 81–200 mm FL, fed on fish and large crustaceans. Daily growth rings were counted on the sagitta of juvenile bluefish. Spawning dates, backcalculated from these counts, suggest that fish captured in the Marsh River (1990–1991) originated from a spring spawning (March–May), and fish captured in Sagadahoc Bay (1990) originated from a summer spawning (predominantly June). We do not believe that these spring and summer spawned fish originated from the known major spring and summer spawning grounds in the South and Mid-Atlantic Bights, respectively. The time required to swim from even the northern portion of these major spawning grounds to the site of capture exceeds the known age of the fish derived from counting daily growth rings. The results suggest that both major spawning areas have been extended to the northeast, or unknown spawning areas exist closer to Maine.

Manuscript accepted 7 January 1994.
Fishery Bulletin 92:494–508 (1994).

Bluefish, *Pomatomus saltatrix*, are widely and irregularly distributed along the continental shelf in temperate and warm water regions (Briggs, 1960; Wilk, 1977). On the Atlantic coast of North America the species is particularly abundant in southern Florida, North Carolina, Virginia, and from New Jersey to southern Massachusetts, where it is highly sought by salt water recreational anglers for its superior fighting qualities. Stray adult bluefish have been reported during the summer in New Brunswick waters (Bay of Fundy, Passamaquoddy Bay, St. Johns River) and the south shore of Nova Scotia (Scott and Scott, 1988). In the Gulf of Maine, the abundance of bluefish has fluctuated widely over time (Bigelow and Schroeder, 1953). During the mid-1970's, an increase in abundance resulted in the development of a major recreational fishery for adult fish in Maine. This increase is reflected in the incidental bluefish catch recorded since 1986 from gillnet fishing activity for more desirable commercial species (cod, etc.): 46.9 metric tons (t) (1986); 8.8 t (1987); 3.9 t (1988); 34.6 t (1989); 24.4 t (1990); 51.9 t (1991): 37.0 t (1992).[1]

Both shore and boat-based recreational fisheries exploit young bluefish (age 0 and 1) in the South Atlantic. More than 75% of the shore-based recreational catch along the south and mid-Atlantic coasts are juvenile fish (age 0).[2] Although isolated reports of juvenile bluefish have been reported in Maine waters (Bigelow and Schroeder, 1953; Lund, 1961; Targett and McCleave, 1974), no information is available on the distribution, food, and age of these fish. The objectives of this study were 1) to review and summarize unpublished locations where juvenile bluefish have been captured between the Piscataqua River (Maine-New Hampshire border) and Passamaquoddy Bay (Maine-New Brunswick border), 2) to characterize the diet of juvenile bluefish in Maine, and 3) to derive parent spawning dates and possible spawning locations from counts of daily growth rings on juvenile bluefish otoliths obtained in Maine.

Materials and methods

Records of juvenile bluefish in Maine

Unpublished records of juvenile bluefish along coastal Maine were reviewed. Sightings were considered reliable if we actually observed the specimens of juvenile bluefish reported or if the observers could

[1] Morrill, R. NMFS Port Agent, Portland, Maine. Personal commun., 1993.

[2] Crecco, V., M. Terceiro, and C. Moore. 1987. A stock assessment of Atlantic coast bluefish, *Pomatomus saltatrix*. Special report prepared for the Atlantic States Marine Fisheries Commission, Washington, D.C., 86 p.

correctly identify preserved juvenile bluefish from the laboratory fish collection.

Study locations

The primary sampling sites were in the Marsh River (a tributary of the Sheepscot River in Newcastle, Maine) near the confluence of Sherman Lake Outlet and Deer Meadow Brook (Fig. 1A). These sites were selected because juvenile bluefish were consistently captured there in preliminary netting experiments conducted during the summers of 1986–89. The sites are approximately 6.5 km from the confluence of the Marsh River and the Sheepscot River and 34.3 km from the mouth of the Sheepscot River. Marsh banks abut the meandering river and mud flats slope from the base of these banks to the edge of the riverbed. The riverbed is about 46–49 m wide at low tide. The mean tidal range is 1.60 m (U.S. Dep. Commer., 1990–91).

Juvenile bluefish were also obtained from sampling sites at Kennebec Point (Fig. 1B) and Merepoint Bay (Fig. 1C). The Kennebec Point site is used routinely by the Division of Benthic and Demersal Fisheries (State of Maine, Dep. of Marine Resources, W. Boothbay Harbor, Maine 04575) to monitor biweekly variation in species diversity and abundance; occasionally, juvenile bluefish were captured there. The site consists of a sandy beach and a small cove, 1.8 km from open ocean. The mean tidal range is 1.37 m (U.S. Dep. Commer., 1990–91).

Abundant schools of juvenile bluefish and clupeids inhabit the Merepoint Bay site, located in shallow water between the floats at Paul's Marina (Fig. 1C). This site is 16.7 km from open ocean and the tidal range is 1.46 m (U.S. Dep. Commer., 1990–91).

Sampling gear

Gill nets were employed to capture juvenile bluefish in the Marsh River for the following reasons. First, the fish were dispersed and sporadic in occurrence and other methods of capture would probably have produced few fish. Swift tidal currents prevented the use of seines at other than low slack water, and a seine requires two operators and frequently only one was available.

Two sinking gill nets (Sterling Marine Products, Jonesport, Maine 04649), measuring 2.4 m in depth and 48.8 m in length, were suspended between stakes driven into the banks of the Marsh River. Ropes suspending these nets bifurcated 4.6 m from the end of each net; one length was attached to the float line and the other to the lead line. Poles measuring 2.1 m were positioned between the float and lead lines at each end of each net to prevent the nets from collapsing and twisting during rapid tidal flows at mid-ebb and mid-flood. A window weight (2.4 kg) was attached to the lower end of each pole to maintain the net vertically. One net was a variable mesh type constructed from two 6.1-m panels of each of the following square mesh sizes: 1.27 cm, 1.90 cm, 2.54 cm, and 3.18 cm. Individual panels were randomly positioned. Additional floats were attached to the float line of these sinking nets so they fished approximately 15–30 cm below the surface. This enabled floating debris to pass over the net. The second net was constructed entirely of 1.27-cm square mesh.

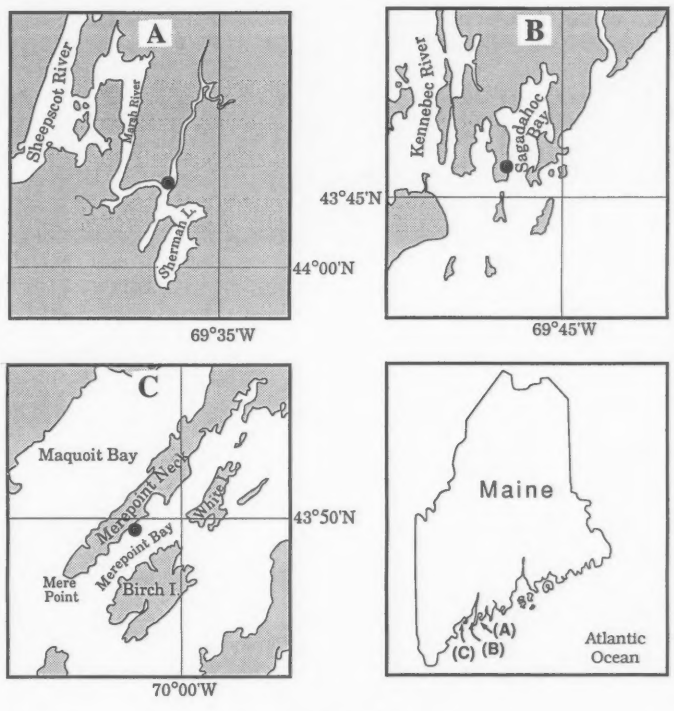


Figure 1

Sampling locations for juvenile bluefish, *Pomatomas saltatrix*, in (**A**) Marsh River, (**B**) Sagadahoc Bay, and (**C**) Merepoint Bay, Maine.

Beginning in June, gill nets were fished for approximately four hours, once a week, until catches revealed that bluefish were present in the river. The nets were then fished two or three times a week. Fishing was again reduced to one set per week in September when no further catches of bluefish were made. When two weeks of fishing produced no juvenile bluefish, fishing was discontinued. Gill nets were set in the Marsh River on 20, 27 June; 4, 11, 18, 25 July; 1, 6, 14, 16, 21, 22, 23, 27, 28, 30 August; 5, 6, 11, 12, 18, 20, 26 September; 3, 12 October 1990 and 20, 26 June; 9, 17, 22, 25, 29 July; 1, 6, 12, 15, 22, 29 August; 4, 5, 10, 12, 17 September; and 1, 8 October 1991. When bluefish were present, the net was inspected every 30 minutes without pulling and resetting it. All fish were removed from the net, identified to species, and measured to the nearest mm.

Juvenile bluefish were captured by beach seine on 10 August 1990 and 27 September 1991 at Kennebec Point. The seine was constructed of 6.35-mm square mesh and measured 1.2 m × 15.2 m. It was hauled a horizontal distance of 152.4 m on each sampling date. Fish were also collected at Kennebec Point on 22 August 1990 in a fyke net constructed of 6.35-mm square mesh with two 15.2-m wings. The fyke net was set in a dry channel at low tide, and a 3-hour set was initiated when the incoming tide first reached the hoops. Juvenile bluefish were captured at Merepoint on 9 September 1991 by using the variable mesh gill net described previously.

Field and laboratory data recorded

Fishing time was recorded during each sampling trip to the Marsh River. The set was initiated when the net was set, attached to stakes, and spread. Termination of the set occurred when the net was detached from one stake. Temperature and salinity were recorded at the surface and bottom with a YSI Model 33 SCT Meter immediately following the beginning of a set and just prior to the end of a set. Tide condition, time of slack water (if it occurred), and maximum depth noted from graduations on the SCT cable were also recorded.

Both individuals and schools (two or more gilled in close proximity) of juvenile bluefish were captured in the gill nets. The fish were stored in plastic bags containing information on time of capture (to the nearest 30 minutes), date of capture, and mesh size of the capture panel. Fish were stored in an ice cooler until returned to the laboratory.

Within nine hours of capture, fish were wiped with paper towels and weighed to the nearest 0.1 gram. Both total length (TL) and fork length (FL) (Hubbs and Lagler, 1958) were recorded to the nearest millimeter. Stomachs were removed and frozen in small scintillation vials. Heads were refrigerated until the sagitta were removed.

Daily growth rate was derived from the total increase in length divided by the number of daily growth increments counted. Total growth in length is equivalent to size (FL) at capture minus the approximate size at hatching (2 mm, Deuel et al., 1966).

Treatment and analysis of stomach contents

Stomachs were thawed and submerged in 3% sea water formalin for approximately 19 hours to harden stomach contents. Stomachs were then rinsed several times with sea water and their contents were identified to the lowest taxon, counted, blotted on a paper towel, and weighed to 0.0001 grams. Stomach contents were then refrozen and freeze-dried (Labconco Freeze Dryer 8) for 48 hours at –40°C under a vacuum of approximately 25 microns mercury (Hg). Dry weights were recorded to the nearest 0.0001 gm.

Three prey item indices were computed to reduce potential bias associated with a single index (Hynes, 1950; Windell, 1971; Friedland et al., 1988). We employed the methodology of Friedland et al. (1988) in computing 1) the number of stomachs in which a species occurred expressed as a) a percentage of the total number of stomachs containing food (F=percent frequency of occurrence) and b) a percentage of the total number of stomachs examined (F1=percent frequency of occurrence); 2) the number of individuals of each prey species expressed as a percentage of the total number of food items (N=percent numerical abundance); and 3) the wet weight of a species expressed as a percentage of the total wet weight of food items (W=percent wet weight) and the dry weight of a species expressed as a percentage of the total dry weight of food items (W1=percent dry weight).

Preparation and analysis of otoliths

Saggita were removed from each fish within 24 hours of capture. Excess tissue was removed with forceps. Pairs of sagitta were stored in 7-mL scintillation vials for 1–3 months prior to mounting and ageing. Each sagitta was mounted concave side down on a microscope slide with Epo-Kwick (Buehler Ltd., Lake Bluff, Illinois). Commercial grade wet-dry sandpaper (600 grit or 24 μ) was used for initial coarse sanding. Final sanding and polishing was performed with 9-μ and 0.3-μ wet-dry sandpaper respectively (Buehler, Ltd). The addition of a small drop of glycerine to the surface of the polished otolith assisted in the resolution of daily growth rings. Three replicate counts were performed during one day by one

reader using a compound microscope with transmitted polarized light at 100–200×. Counts were rarely accomplished in a straight line; it was usually necessary to traverse the otolith in either a general dorsal or ventral direction to complete a count because daily growth rings in many portions of the otolith are obscure. Each counting pathway was usually different. The criterion of Nyman and Conover (1988) was used: if one of three counts differed by >10%, an additional count was performed and the value that differed by >10% was discarded. The mean of the three remaining counts was recorded. Dates of first ring deposition for juvenile bluefish collected from all sources were backcalculated from the number of growth increments counted.

Estimates of swimming speed and swimming distance

The distance juvenile bluefish were capable of swimming per day was calculated from estimates of the average body length during migration and the relationship between swimming speed and average body length. Average body length was equal to one-half the mean size of fish collected during a 2-week period immediately following first appearance at a sampling site minus 2 mm, the size at hatching (Deuel et al., 1966). The swimming speed for fish such as salmon, cod, and herring is about three times the body length/sec for fish measuring 10–100 mm (Harden Jones, 1968). Juvenile bluefish measuring 155–213 mm TL swam at speeds averaging 94 mm/sec at 20°C and 180–260 mm/sec when cooler water was added (Olla et al., 1985). We estimated swimming speed of juvenile bluefish at no more than 2 body length/sec.

The mean size of juvenile bluefish collected from the Marsh River during a 2-week period immediately following their first appearance in 1990 and 1991 was 108 mm FL (n=17) and 101 mm FL (n=19). Total growth between hatching and appearance at the collection site in 1990 was 106 mm (108 mm minus 2 mm [the size at hatching]) and in 1991, 99 mm. The average size of the fish during this migration would be one-half these values or 53 and 50 mm. Swimming distances per day during migrations in 1990 and 1991 were 53 mm × 2 (twice the body length) = 106 mm/sec (9.16 km/day) and 50 mm × 2 = 100 mm/sec (8.64 km/day). Similarly, the mean size of juvenile bluefish collected from Sagadahoc Bay during August 1990 was 48 mm FL (n=29). The swimming distance per day was therefore 23 mm × 2 = 46 mm/sec (3.97 km/day).

The shortest distances between the northern portions of the spawning grounds in the South Atlantic Bight to the collection site in the Marsh River and the Middle Atlantic Bight to the collection site in Sagadahoc Bay were estimated at 1350 km and 425 km respectively.

Statistical analysis

The relationship between fork length and the number of daily rings for juvenile bluefish captured in Maine during 1990–91 was described by linear regressions, where X is the $\log_{10}$ of fork length and Y is the number of daily rings. Slopes were then compared with ANCOVA. The curvilinear relationship of the same data from Maine (1990–91) and New York (1985–86) was described by quadratic equations, where X is fork length and Y is number of daily rings. The relationship of fork length to growth rate for combined data from Maine was described by a linear regression, where X is the fork length and Y is the rate of growth.

Results and discussion

Records of juvenile bluefish from the coast of Maine

Most records of juvenile bluefish were from southwestern Maine (York, Cumberland, Sagadahoc, and Lincoln counties) during the months of July, August, and September (Table 1). Fish varied in size from 37 to 197 mm FL (39–218 mm TL) from both oceanic and estuarine environments. Atlantic puffins (*Fratercula arctica arctica*), Arctic terns (*Sterna paradioaea*), and roseate terns (*Sterna dougallii dougalli*) were reported as feeding on young-of-year bluefish in July near Matinicus Rock and Seal Island (Knox County).[3] These observations indicated that juvenile bluefish occur in the offshore waters of Maine prior to their usual appearance inshore during August–September. Clark (1973) observed that juvenile bluefish remain where salinities are high when they first arrive, and later, as summer progresses, they penetrate into estuaries. Little Kennebec Bay (Table 1, No. 28) is the most northeast location where the capture of juvenile bluefish was confirmed. Three juvenile bluefish were among 1,000 age-1 Atlantic herring, *Clupea harengus*, tagged at this location on 25 August 1983 (Creaser and Libby, 1986).

Young-of-year (YOY) bluefish may be more abundant northeast of Boothbay Harbor than suggested by Table 1. The scarcity of information from this area

[3] Kress, S. Cornell Univ. Ornithology Lab, Ithaca, NY. Personal commun., January 1991.

Table 1

Unpublished records of juvenile bluefish, *Pomatomas saltatrix*, in Maine.

Location	N. Lat.	E. Long.	Date of capture	Oceanic (O) or estuarine (E)	No. captured	Size (mm)[1] TL	Size (mm)[1] FL	Method of capture[2]
Wells Harbor (York Co.)								
1 Wells Harbor	43°19"	70°34'	Aug 1991	E	1	68		FN
Old Orchard Beach (York Co.)								
2 1 Mile off Amusement Pier	43°31'	70°21'	Summer 1961–1964	O	—	Juvenile		HL
Scarborough Marsh (Cumberland Co.)								
3 Confl. of Dunston, Libby, Nonesuch R.	43°33'	70°20'	Summer 1987	E	—	Juvenile		HL
Portland Harbor (Cumberland Co.)								
4 Union Wharf	43°39'15"	70°15'	Sept 1984	O	6	150–200		HL
5 SMVTI Dock	43°39'	70°14'15"	Sept 1986	O	—	130–150		HL
Royal River (Cumberland Co.)								
6 Royal River	43°47'30"	70°10'	Summer 1988	E	—	Juvenile		—
Merepoint (Cumberland Co.)								
7 Merepoint Bay	43°50'	70°00'01"	26 Sept 1991	E	97	150–174		GN
Jenny Island, Casco Bay (Cumberland Co.)								
8 Jenny Island	43°46'	69°55	16 July 1991	E	1	40		CT
New Meadows River (Cumb.-Sagadahoc Co.)								
9 Howard Pt., Thomas Bay	43°53'15"	69°53'10"	Aug 1988	E	3	70–130		FK
Kennebec River (Sagadahoc Co.)								
10 Atkins Bay	43°45'	69°48'	Summer 1981	E	—	80–90		HS
11 Winnegance Bay	43°53'	69°49'	Summer 1988–1990	E	—	50–150		HL
12 Bath Bridge	43°55'	69°48'30"	Summer 1982	E	90	<100		OT
13 Mouth of Androscoggin R.	43°57'	69°53'	5 Aug 1983	E	2	82–86		HS
14 Mouth of Abagadasset R.	44°00'30"	69°51'	17 July 1986	E	5	70–77		HS
Mouth of Abagadasset R.			11 Sept 1987	E	2	142–150		HS
Mouth of Abagadasset R.			3 Aug 1989	E	8	52–76		HS
Mouth of Abagadasset R.			3 July 1991	E	6	112–115		HS
Mouth of Abagadasset R.			18 July 1991	E	2	84–94		HS
Sagadahoc Bay (Sagadahoc Co.)								
15 Kennebec Pt.	43°45'20"	69°45'45"	10–22 Aug 1990	O	29	39–70	37–64	HS
Montsweag Bay (Lincoln Co.)								
16 Berry Island	43°58'15"	69°40'55"	30 Aug 1972	E	1	112		HS
Berry Island			29 Aug 1973	E	2	132–141		HS
Berry Island			8 Sept 1974	E	4	125–140		HS
Sheepscot River (Lincoln Co.)								
17 Cross River	43°55'	69°37'	8 Aug 1991	E	1	115		HS
18 The Eddy	43°59'30"	69°39'	9 July 1991	E	3	80–85		HS
19 Marsh River	44°01'	69°35'45"	14 Aug 1986	E	28	93–121		GN
Marsh River			26 Aug 1987	E	6	129–163		GN
Marsh River			8–28 Aug 1989	E	102	92–194		GN
Marsh River			1 Aug–26 Sept 1990	E	149	89–218	81–197	GN
Marsh River			17 July–17 Sept 1991	E	60	101–217	193–196	GN
20 Sheepscot Falls	44°02'45"	69°37'	Aug 1967	E	—	150–200		HL
21 Sheepscot River (town of Sheepscot)	44°03'30"	69°36'30"	2 Aug 1989	E	1	140		HL
Boothbay Harbor (Lincoln Co.)								
22 Lobster Cove	43°51'	69°37'	30 Aug 1990	O	1	145	131	HL
Lobster Cove			11 Aug 1991	O	4	162–192		HL
23 Townsend Gut	43°50'	69°39"	5 Sept 1985	O	1	Juvenile		HL
24 DMR Dock	43°50'45"	69°38'30"	14 Sept 1971	O	5	95–105	89–97	—
DMR Dock			25 Aug 1978	O	1	86		DN
DMR Dock			4 July 1984	O	3	40–50		HL
25 Foot Bridge	43°51'	69°37'40"	Summer 1970–1974	O	—	Juveniles (2 sizes)		HS
Matinicus (Knox Co.)								
26 Matinicus Rock	43°47'	68°51'30"	18 July 1986	O	1	77		AP
Matinicus Rock			5 July 1989	O	2	85–90		AP
Matinicus Rock			Mid July 1990	O	2	30–40		AT
Matinicus Rock			9–17 July 1991	O	14	40–50		AT

Table 1 (Continued)

Location	N. Lat.	E. Long.	Date of capture	Oceanic (O) or estuarine (E)	No. captured	Size (mm)[1] TL	Size (mm)[1] FL	Method of capture[2]
Matinicus Rock			24–30 July 1991	O	4	50–60		RT
Seal Island (Knox Co.)								
27 Seal Is.	43°53'	68°45'	July 1991	O	1	50		AT
Little Kennebec Bay (Washington Co.)								
28 Marston Pt.	44°39'	67°26'15"	25 Aug 1983	O	3	100–130		HW

[1] TL = total length; FL = fork length.
[2] OT = Otter trawl; FN = Fyke net ; HL = Hook and line; — = Unknown; HS = Haul seine ; AP = Atlantic puffin; GN = Gill net; AT = Artic tern; DN = Dip net; CT = Common tern ; HW = Herring weir; RT = Roseate tern.

may result from the lack of scientific fish sampling activity and lack of familiarity with the identification of juvenile bluefish by the sportfishing public and finfish processors. Clark (1973) attributed high densities of juvenile bluefish in areas such as South Carolina and the New York Bight to sampling activity and availability of records from those areas.

Some published information exists on the distribution of juvenile bluefish in southwestern Maine. They have been reported from Casco Bay (Bigelow and Schroeder, 1953; Wilk, 1977), Boothbay Harbor (Lund, 1961) and Montsweag Bay (Targett and McCleave, 1974).

Length-frequency distributions

Length-frequency distributions of juvenile bluefish captured in the Marsh River (1990–91), Sagadahoc Bay (1990), and Merepoint Bay (1991) varied between 8 and 20 cm, 3 and 6 cm, and between 14 and 17 cm respectively (Fig. 2, A–D). Length-frequency data from the Marsh River was combined in 1-cm groupings and presented as one figure per year because fish were collected for only two months. Although the size range recorded during both 1990 and 1991 was similar, larger juveniles were more prevalent during 1991 (Fig. 2, A and B). The length-frequency composition of fish captured by beach seine from Sagadahoc Bay on 10 and 22 August 1990 (Fig. 2C) confirms the presence of small juveniles of 3–6 cm FL in Maine waters.

Previous reports of juvenile bluefish less than 70 mm from Wells Harbor, Winnegance Bay, the mouth of the Abagadasset River, Boothbay Harbor, Matinicus Rock and Seal Island have been presented in Table 1. The overall length-frequency range (8–20 cm FL) reported for fish captured in the Marsh River during 1 August–26 September 1990 and 17 July–17 September 1991 was similar to the length-frequency range reported from Great South Bay, New York (8–22 cm FL) during 28 May–12 August 1985 and 10 June–20 August 1986 (Nyman and Conover, 1988). Length-frequency distributions generated from gillnet catches (Fig. 2, A, B, D) are biased because panels of individual mesh sizes in gill nets are selective for specific sizes of fish.

Temperature and salinity data collected during gillnet sets

Juvenile bluefish were captured on both incoming (I) and outgoing (O) tides between 1 August and 26 September 1990 and between 17 July and 17 September 1991. Specific water temperatures do not appear to be associated with the arrival and departure of juvenile bluefish. Bluefish were first captured at water temperatures of 24.6–27.0°C (1990) and 22.8–24.0°C (1991). None were captured when the temperature dropped below 16.0°C (1990) and 19.3°C (1991). Water temperatures varied between 16.0 and 27.0°C (1990) and between 19.3 and 27.4°C (1991) when bluefish were present.

Lund and Maltezos (1970) reported that juveniles and adults appear at temperatures of 12–15°C and depart at temperatures of 13–15°C. Oben (1957) reported that juveniles appear at temperatures of 18–24.5°C and depart at 13–15°C. Similarly, Nyman and Conover (1988) reported that juveniles appear at 20–24°C and depart at water temperatures in the "middle-teens." We believe that juvenile bluefish arrived at the mouth of the Sheepscot River when the water temperature was relatively low and they were attracted to the Marsh River, 34.3 km upstream, by the warmer water. These fish appeared to remain in the Marsh River until the water temperature dropped to a temperature range that was lower than the water temperature at the time of their arrival in the sampling area.

The salinity of the Marsh River varied between 9.5 and 23.3 ppt (1990) and between 9.6 and 26.5 ppt (1991) when juvenile bluefish were present.

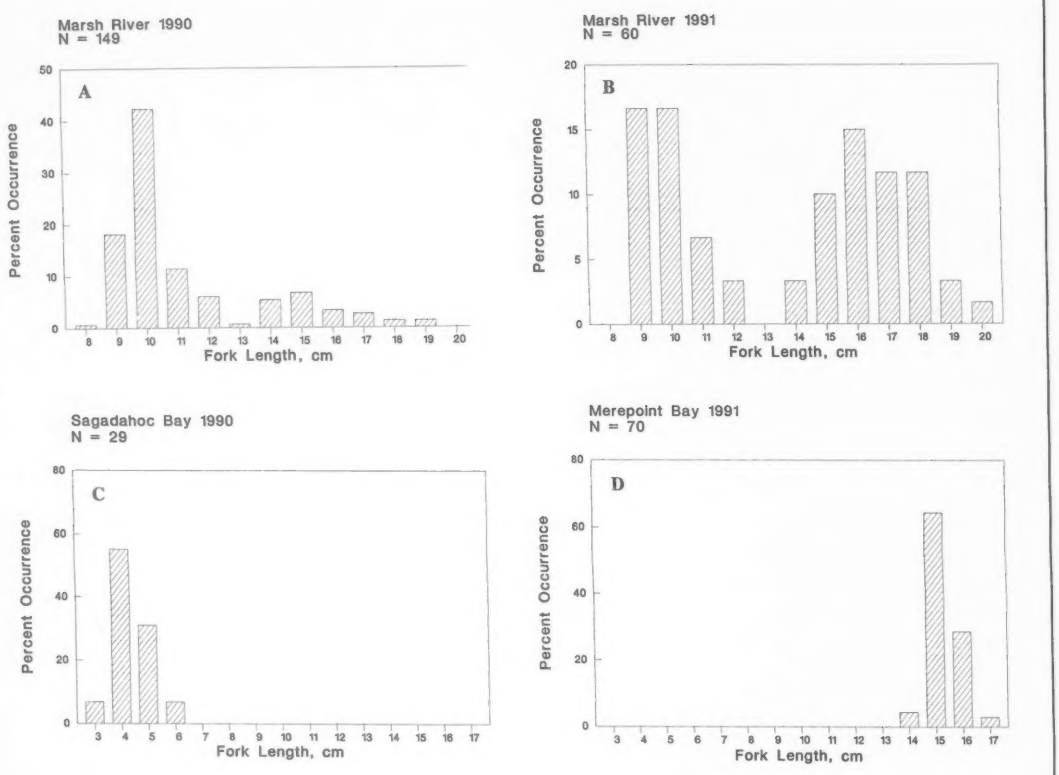


Figure 2

Length-frequency histograms for juvenile bluefish, *Pomatomas saltatrix*, collected in Maine: (**A**) Marsh River 1 Aug.–26 Sept. 1990; (**B**) Marsh River 17 July–17 Sept. 1991; (**C**) Sagadahoc Bay 10–22 Aug. 1990; and (**D**) Merepoint Bay 26 Sept. 1991.

Smale and Kok (1983) collected juveniles at 12–35 ppt, Clark (1973) occasionally found bluefish in very brackish water, and Baird (1873) captured juveniles from the freshwater portion of tidal rivers.

Stomach contents

Stomach contents of juvenile bluefish (81–200 mm FL) collected from the Marsh River in 1990 and 1991 are presented in Table 2. During 1990, fish were present in 81.4% of stomachs containing food (F), crustaceans in 39.5% (F), and plant material in 4.7% (F). During 1991, crustaceans were slightly more prevalent than fish. Crustaceans were present in 69.0% of stomachs containing food (F), fish in 62.1% (F), and plant material in 5.2% (F). The frequency of occurrence of polychaetes was 3.4% (F) and of insects, 1.7% (F).

During 1990 and 1991, crustaceans were the predominant prey items in terms of numbers of individuals observed (N) expressed as a percent of the total number of prey items recorded. Crustaceans composed 58.0% (1990) and 83.4% (1991) of the total prey items, fish composed 39.9% (1990) and 11.3% (1991), and plant material 2.0% (1990) and 4.5% (1991). During 1991, 0.5% and 0.3% of the total number of prey items were polychaetes and insects.

During 1990 and 1991, fish were the predominant prey in terms of wet or dry weight expressed as a percentage of the total wet weight (W) or dry weight (W1) of all prey species recorded. Fish composed 77.4% of total wet weight (W) and 79.9% of total dry weight (W1) during 1990 and 61.9% (W) and 67.5% (W1) during 1991. Crustaceans composed 22.5% (W) and 20.0% (W1) during 1990 and 37.3% (W) and

Table 2

The stomach contents of 149 juvenile bluefish, *Pomatomas saltatrix*, measuring 81–197 mm FL ($\bar{x}$=117 mm), and 60 juveniles measuring 93–200 mm FL ($\bar{x}$=142 mm), collected from the Marsh River, Maine, during 1 August–26 September 1990 and 17 July–17 September 1991, respectively.

	Marsh River 1990					Marsh River 1991				
Taxon	F (%)[1]	F1 (%)[2]	N (%)[3]	W (%)[4]	W1 (%)[5]	F (%)	F1 (%)	N (*) (%)	W (%)	W1 (%)
Class Crustacea										
Argulus sp.	1.550	1.342	1.024	0.021	0.027					
Corophium sp.						1.724	1.667	0.263 (0.606)	0.011	0.009
Crangon septemspinosa	34.884	30.201	55.631	22.351	19.888	63.793	61.667	26.579 (61.212)	37.294	31.830
Rhithropanopus harrisii	0.775	0.671	0.341	0.061	0.064					
Unidentified Crustacea	1.550	1.342	0.683	0.063	0.031					
Unidentified Isopoda	0.775	0.671	0.341	0.029	0.037					
Zoea of Majidae sp.						3.448	3.333	56.579	0.006	0.005
Total	39.535	34.228	58.020	22.525	20.046	68.966	66.667	83.421 (61.818)	37.310	31.844
Class Osteichthyes										
Alosa pseudoharengus	6.202	5.369	4.096	13.751	13.953					
Clupeidae spp.	5.426	4.698	2.730	7.392	8.045	15.517	15.000	3.158 (7.273)	27.131	29.792
Fundulus heteroclitus	0.775	0.671	0.683	7.309	9.239	1.724	1.667	0.526 (1.212)	6.720	7.366
Menidia menidia	9.302	3.054	5.119	13.229	13.798	8.621	8.333	1.579 (3.636)	2.471	2.228
Fish remains	59.690	51.678	27.304	37.739	34.861	36.207	35.000	6.053 (13.939)	25.589	28.146
Total	81.395	70.470	39.932	77.421	79.895	62.069	60.000	11.316 (26.061)	61.911	67.532
Class Polychaeta										
Polychaete remains					3.448	3.333	0.526	(1.212)	0.445	0.342
Total					3.448	3.333	0.526	(1.212)	0.445	0.342
Class Insecta										
Hymanoptera (unident.)					1.724	1.667	0.263	(0.606)	0.009	0.005
Total					1.724	1.667	0.263	(0.606)	0.009	0.005
Plant material										
Leafy	0.775	0.671	0.341	0.005	0.007					
Woody	3.986	3.356	1.706	0.049	0.052	5.172	5.000	4.474 (10.303)	0.325	0.278
Total	4.651	4.027	2.048	0.054	0.059	5.172	5.000	4.474 (10.303)	0.325	0.278
Number of stomachs examined				149				60		
Number of stomachs containing food (% containing food)				129 (86.58)				58 (96.67)		
Number of empty stomachs (% empty)				20 (13.42)				2 (3.33)		
Mean wet weight/stomach (all stomachs) gm				0.651				1.133		
Mean dry weight/stomach (all stomachs) gm				0.116				0.183		
Mean wet weight/stomach (stomachs with food) gm				0.752				1.172		
Mean dry weight/stomach (stomachs with food) gm				0.134				0.189		

[1] F = % frequency of occurrence — the number of stomachs in which a species (taxon) occurred expressed as a % of the total number of stomachs containing food.
[2] F1 = % frequency of occurrence — the number of stomachs in which a species (taxon) occurred expressed as a % of the total number of stomachs examined.
[3] N = % numerical abundance — the number of individuals of each species (taxon) expressed as a % of the total number of food items (individual prey in stomachs) (*) designates the % numerical abundance excluding 215 zoea of Majidae found in the stomachs of two fish.
[4] W = % weight — wet weight of a species (taxon, prey category) expressed as a % of the total wet weight of food items.
[5] W1 = % weight — dry weight of a species (taxon, prey category) expressed as a % of the total dry weight of food items.

31.8% (W1) during 1991. Plant material accounted for 0.1% (W) and 0.1% (W1) during 1990 and 0.3% (W) and 0.3% (W1) during 1991. Polychaetes made up 0.4% (W) and 0.3% (W1) during 1991; insects made up 0.01% (W) and 0.01% (W1).

Stomach contents of juvenile bluefish collected from other areas in Maine during 1990 and 1991 are presented in Table 3. Bluefish measuring 150–173 mm FL were captured from Merepoint Bay on 9 September 1991. Fish were the predominant prey item

for all indices: 80.0% (F), 67.7% (N), 85.0% (W), and 88.6% (W1). Crustaceans composed 24.0% (F), 32.3% (N), 15.0% (W), and 11.4% (W1).

Bluefish measuring 37–64 mm FL were captured from Sagadahoc Bay on 10 and 22 August 1990. The predominant prey items recorded from these small juveniles were crustaceans (mysids and copepods). The frequency of occurrence of mysids and copepods in stomachs containing food (F) was 10.3% and 96.6%, respectively. Crustaceans were also the predominant prey items in terms of their wet or dry weight, expressed as a percentage of the total wet weight (W) or dry weight (W1). Crustaceans composed 82.2% of the total wet weight (W) and 80.0% of the total dry weight (W1). Fish remains were a minor constituent of the stomach contents of these small bluefish; they occurred in 6.9% of stomachs containing food (F). Fish also composed 17.7% of the total wet weight (W) and 21.0% of the total dry weight (W1). No information was available regarding the numbers of individuals observed (N) expressed as a percent of the total number of prey items recorded because copepod remains were so numerous that it was impractical to count them.

The diet of juvenile bluefish collected from the Marsh River in 1990 and 1991 and from Merepoint Bay in 1991 is consistent with observations by Breder (1922), Grant (1962), data for bluefish >10 cm reported by Smale and Kok (1983), and the 1981 results recorded in Friedland et al. (1988). All studies showed that the major portion of the diet (by weight or volume) of juvenile bluefish ≥8 cm in length consisted of fish. Although results presented by Lassiter (1962) and Naughton and Saloman (1984) are also consistent with this observation, Lassiter (1962) did not report bluefish lengths and some of the bluefish in Naughton and Saloman's (1984) data were older than age 1 (e.g. 39.9 cm).

Our findings regarding the diet of juvenile bluefish collected from Sagadahoc Bay (1990) were consistent with results presented by Kendall and Naplin (1981) and Smale and Kok (1983) for bluefish <100 mm. Smale and Kok (1983) reported that juvenile bluefish <100 mm feed predominantly on small crustaceans, and Kendall and Naplin (1981) stated that most of the diet of juvenile bluefish ($\bar{x}$=4.33 mm) consisted of copepods, copepodites, cladocera, and fish eggs. A transition to pisciverous feeding by juvenile bluefish at a size range between 60 and 100 mm has been reported (Nichols, 1913; Greeley, 1939; Oben, 1957; Clark, 1973; Smale and Kok, 1983). The transition to fish as prey had not yet occurred in bluefish measuring 37–64 mm from Sagadahoc Bay (Table 3).

On a per cent weight basis, the dominant prey species of juvenile bluefish (81–200 mm FL) collected from the Marsh River and Merepoint Bay included the mud shrimp *Crangon septemspinosa*, juvenile alewives, *Alosa pseudoharengus*, unidentified clupeids, Atlantic silversides, *Menidia menidia*, mum-

Table 3

The stomach contents of 34 juvenile bluefish, *Pomatomas saltatrix*, measuring 150–173 mm FL ($\bar{x}$=156 mm), collected from Merepoint Bay on 9 September 1991, and 29 small juveniles, measuring 37–64 mm FL ($\bar{x}$=48 mm), collected from Sagadahoc Bay, Maine, on 10 and 22 August 1990.

	Merepoint Bay 1991					Sagadahoc Bay 1990				
Taxon	F(%)	F1(%)	N(%)	W(%)	W1(%)	F(%)	F1(%)	N(%)	W(%)	W1(%)
Class Crustacea										
Crangon septemspinosa	24.000	17.647	32.258	14.973	11.400					
Mysidacea spp.						10.345	10.345	—	13.411	14.360
Copepod remains						96.552	96.552	—	68.746	64.621
Total	24.000	17.647	32.258	14.973	11.400	106.897	106.897		82.157	79.981
Class Osteichthyes										
Fish remains	68.000	50.000	58.065	40.057	42.353	6.897	6.897	—	17.742	21.019
Clupeidae spp.	12.000	8.824	9.677	44.970	46.247					
Total	80.000	58.824	67.742	85.027	88.600	6.897	6.897		17.742	21.019
Number of stomachs examined				34				29		
Number of stomachs containing food (% containing food)				25 (73.53)				29 (100)		
Number of empty stomachs (% empty)				9 (26.47)				0 (0)		
Mean wet weight/stomach (all stomachs) gms				0.48288				0.03057		
Mean dry weight/stomach (all stomachs) gms				0.08890				0.00596		
Mean wet weight/stomach (stomachs with food) gms				0.67367				0.03057		
Mean dry weight/stomach (stomachs with food) gms				0.12091				0.00596		

michogs, *Fundulus heteroclitus*, and unidentified fish remains (Tables 2 and 3). Other authors reported that a significant portion of the juvenile bluefish diet consists of shrimp (Linton, 1905; Wilk, 1977; Friedland et al., 1988), clupeids (Hildebrand and Schroeder, 1928; Greeley, 1939; Grant, 1962; Richards, 1976; Naughton and Saloman, 1984), Atlantic silversides (Hildebrand and Schroeder, 1928; Greeley, 1939; Grant, 1962; Lassiter, 1962; Wilk, 1977; Friedland et al., 1988), and cyprinodontids (Greeley, 1939; Grant, 1962; Wilk, 1977). Prey of minor importance included *Argulus* sp., *Corophium* sp., *Rhithropanopus harrisii*, unidentified crustacea and isopods, zoea of Majidae sp., polychaete remains, unidentified *Hymenoptera*, and both leafy and woody plant material (Table 2). Estuaries in Maine are probably seasonal nursery grounds where high prey densities and warm water temperatures result in rapid growth.

During 1990 and 1991, 13.42% and 3.33% of the fish collected in the Marsh River and 26.47% (1991) of the fish collected in Merepoint Bay possessed empty stomachs (Tables 2 and 3). With the exception of the 16% estimate reported by Grant (1962), who also used gill nets, the percent of empty stomachs reported by several investigators varied between 30 and 87%. Perhaps the low incidence of empty stomachs reported in our studies resulted from the use of gill nets, which constrict the gills and esophagus thus reducing the possibility of regurgitation.

An analysis of daily growth increments on otoliths

Growth increments on the otoliths of many species of juvenile fishes, including bluefish, are produced on a daily basis as long as growing conditions are adequate (Nyman and Conover, 1988). Bluefish collected from the Marsh River displayed 94–200 ($\bar{x}$=126) and 97–176 ($\bar{x}$=134) daily growth increments during 1990 and 1991, respectively. Fish collected from Sagadahoc Bay (1990) displayed 58–93 ($\bar{x}$=66) daily growth increments, and fish collected from Merepoint Bay (1991) displayed 125–146 ($\bar{x}$=134) daily growth increments. First ring deposition occurs approximately 2–4 days after spawning (Nyman and Conover, 1988) so these daily growth increments correspond to a total of approximately 129 days (Marsh River, 1990), 137 days (Marsh River, 1991), 69 days (Sagadahoc Bay, 1990), and 137 days (Merepoint Bay, 1991) of growth after spawning.

Spawning occurs somewhere along the Atlantic coast during practically every month of the year (Table 4). Several "seasonal" periods of significant spawning are evident. Major spawning periods occur during the "spring" (March–May) in the South Atlantic Bight and "summer" (May–September) in the Middle Atlantic Bight. A minor "fall-winter" (Kendall and Walford, 1979) and perhaps "summer-fall" (Collins and Stender, 1987) spawning period also occurs in the South Atlantic Bight.

It is unlikely that juvenile bluefish captured in the Marsh River during the spring and in Sagadahoc Bay during the summer originated from the major spring spawning in the South Atlantic Bight or the major summer spawning in the Middle Atlantic Bight. Most juvenile bluefish from the Marsh River originated from a spring spawning during March–May (Fig. 3, A and B). Conservative estimates of the time required to swim from the northern portion of the spawning ground in the South Atlantic Bight to the collection site in the Marsh River during 1990 and 1991 would equal 147 days (1350 km ÷ 9.16 km/day) and 156 days (1350 km ÷ 8.64 km/day), respectively. These estimates of swimming time exceed the known ages of juvenile bluefish derived from daily ring counts (129 days, 1990; 137 days, 1991) even before additional time from physical and biological factors are considered. These factors include 1) swimming into the current from Cape Hatteras to Southwestern Maine (Bumpus and Lauzier, 1965), 2) the possibility that swimming speed is less than twice the body length, 3) decreased swimming speed at night (Olla et al., 1985), and 4) feeding behavior which results in nonlinear movement.

Juvenile bluefish from Sagadahoc Bay originated from a summer spawning which occurred mainly during June (Fig. 3C). A conservative estimate of the time required to swim from the northern portion of the spawning ground in the Middle Atlantic Bight to the collection site in Sagadahoc Bay during 1990 would equal 107 days (425 km ÷ 3.97 km/day). This estimate greatly exceeds the known age of the fish (69 days). The estimate of swimming time is increased further when physical and biological factors that impede swimming are considered.

We believe that juvenile bluefish collected from the Marsh River and Sagadahoc Bay may be derived from unknown spawning areas closer to Maine. Lyman (1974) stated that "some of their spawning grounds are known but many remain to be discovered along much of the northeast coast." It is also possible that both major spawning areas known to exist in the South and Middle Atlantic Bights, have extended northward. Another possibility is that "larval transport mechanisms and spawning periodicities for bluefish are considerably more complex than previously believed" (Powles, 1981).

The relationship between the $\log_{10}$ of the fork length and the number of daily rings for 1990 and 1991 data is shown in Figure 4. The range of fish

Table 4

Seasonal spawning dates of bluefish, *Pomatomas saltatrix*, in the South and Middle Atlantic Bight.

	Location	Months of spawning												Evidence of spawning	Size
		M	A	M	J	J	A	S	O	N	D	J	F		
South Atlantic Bight															
Collins and Stender (1987)	Cape Canaveral, FL–Cape Fear, NC													larvae present	≤4 mm SL
	Coast of Georgia and Florida													larvae present	≤4 mm SL
Kendall and Walford (1979)	Outer shelf S. Atlantic Bight													larvae present	≤10 mm SL
	Offshore South of Cape Hatteras, NC									fall and winter spawning					
Nyman and Conover (1988)	Long Island, NY													spawning date backcalculated	——
Pierce (1883)	Lake Worth and Juniper Inlet, FL													ripe adults	——
Powles (1981)	Cape Canaveral, FL–Cape Fear, NC													larvae present	no size given
Middle Atlantic Bight															
Baird (1873)	Fort Macon, NJ													ripe and running adults	——
Chiarella and Conover (1990)	Off New York													analysis of gonads	——
DeSylva et al. (1962)	Indian River Inlet, DE													larvae present	4 mm SL
Deuel et al. (1966)	3 miles east of Fire Island Inlet, Long Is., NY													ripe and running female	——
Herman (1963)	Narragansett Bay, RI													larvae present	3.12 mm SL
Kendall and Naplin (1981)	Ocean City, MD													larvae present	4.33 mm SL
Kendall and Walford (1979)	Midway over continental shelf of Mid–Atlantic Bight													larvae present	<10 mm SL
Morse et al. (1987)	Cape Hatteras, NC, to Long Is., NY													larvae present	no size given
Norcross et al. (1974)	Outer shelf off Virginia–N. Carolina													eggs present	——
	Outer shelf off Virginia–N. Carolina													larvae present	2.0–16.5 mm SL
Nyman and Conover (1988)	Hudson River, NY													spawning date backcalculated	——
Pearson (1941)	Mouth of Chesapeake Bay, VA													larvae present	4–7 mm SL
Perlmutter (1939)	Southern Long Island Shore, NY													ripe and running female	——
Sherman et al. (1984)	NE United States													larvae present	3.5–28 mm SL

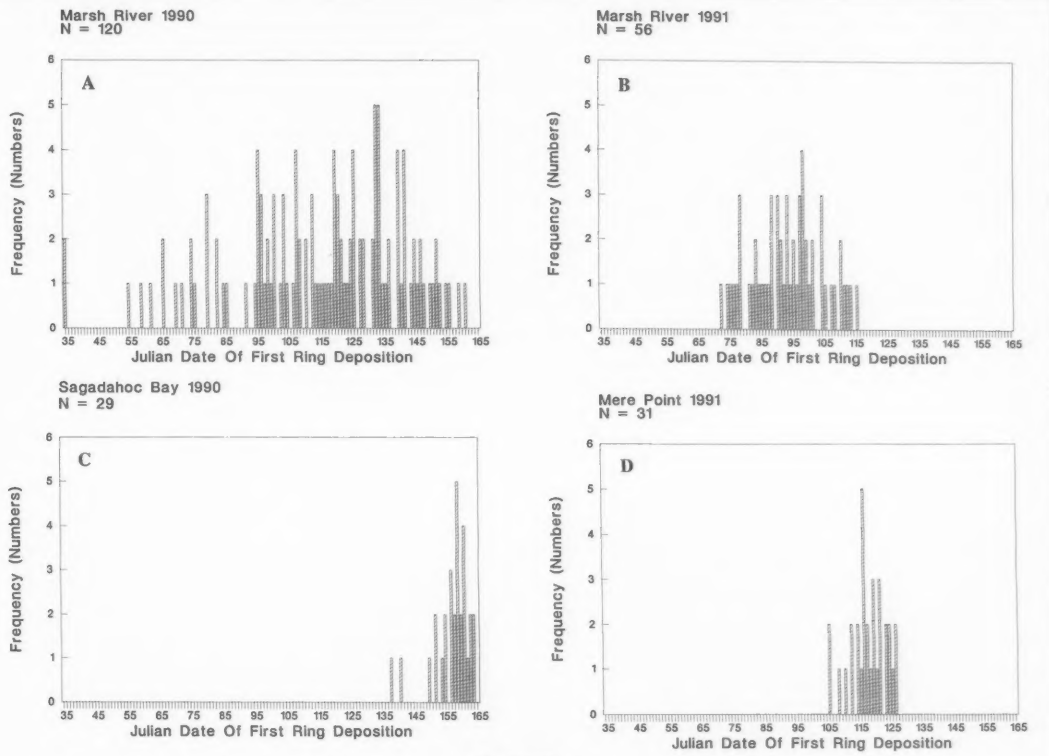


Figure 3

Estimated dates of ring deposition in otoliths of juvenile bluefish, *Pomatomas saltatrix*, collected in Maine: (**A**) Marsh River 1990; (**B**) Marsh River 1991; (**C**) Sagadahoc Bay 1990; and (**D**) Merepoint Bay 1991.

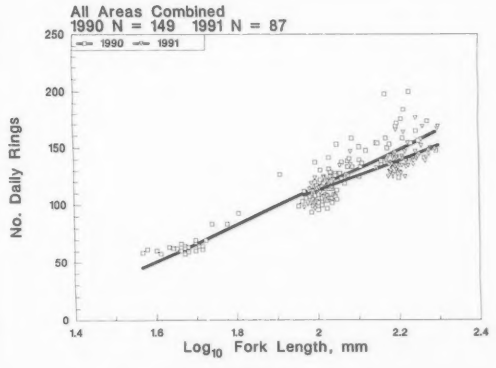


Figure 4

The relationship between $\log_{10}$ fork length (X) and the number of daily rings (Y) for juvenile bluefish, *Pomatomas saltatrix*, captured in Maine during 1990–91. The regression equations are $Y = -209.891 + 162.6751 \log_{10} X$, R^2=0.834, for 1990 and $Y = -151.461 + 132.0466 \log_{10} X$, $R^2 = 0.629$, for 1991.

lengths recorded during 1991 (93–200 mm) was small compared with 1990 (37–197 mm). The number of daily growth rings varied between 58 and 200 (1990) and between 97 and 176 (1991). Although an ANCOVA revealed that the slopes of the relationship of $\log_{10}$ fork length to number of daily rings differed significantly between years ($P<0.05$), the significance of this is questionable because the size range of fish also differed between years. Nyman and Conover (1988) analyzed similar regressions for juvenile bluefish captured in New York waters during 1985 and 1986 and found significant differences in slopes between years. Individual values for fork lengths and daily ring counts collected in New York waters during 1985–1986 obtained from Robert Nyman[4] were fit to quadratic equations and compared to similar values obtained in Maine during 1990–91 (Fig. 5). Fork lengths varied between 41 and 166 mm (1985) and between 31 and 167 mm (1986).

[4] Nyman, R. U.S. Environmental Protection Agency, 401 M St., SW, Washington, DC 20460. Personal commun., June 1991.

The number of daily growth rings varied between 44.3 and 160.0 (1985) and between 42.7 and 133.0 (1986). Fish captured in New York grew faster. This may have resulted from shorter migrations, longer exposure to warm water, or better food or feeding conditions. Raw data plots from which New York information (Fig. 5) were derived are presented in Nyman and Conover (1988, fig. 9).

The growth rate increased from about 0.7 mm/day to about 1.25 mm/day as fish length increased from 50 mm to 200 mm FL (Fig. 6). The mean growth rate was 0.96 mm/day. Nyman and Conover (1988) reported a growth rate of approximately 1.3 mm/day for fish obtained from field collections over a 61-day period.

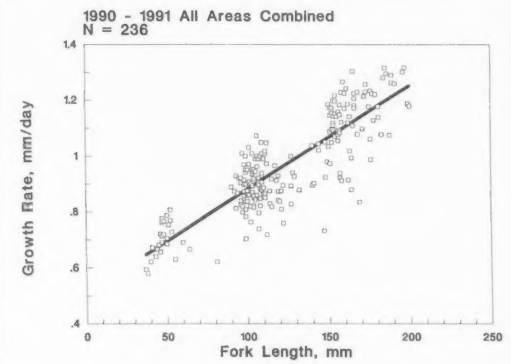


Figure 6

The relationship of fork length to growth rate for juvenile bluefish, *Pomatomas saltatrix*, collected in Maine during 1990–1991. The regression equation is $Y = 0.50990 + 0.00372X$, $R^2 = 0.750$.

Acknowledgments

Numerous scientists, scientific support personnel, and recreational fishermen provided information on sightings of juvenile bluefish in Maine waters. These included Laurie Bean, Eileen Brewer, Lew Flagg, Rod Getchell, Bruce Joule, Jeremy King, Jay Krouse, Jay McGowan, Stuart Sherburne, Malcolm Smith, Thomas Squires, James Stahlnecker, James Thomas, Clement Walton (State of Maine, Dep. of Marine Resources, W. Boothbay Harbor, Maine), Steve Kress (National Audubon Society, Cornell University Ornithology Lab, Ithaca, New York), Michelle Dione (Wells Sanctuary, Wells, Maine), James McCleve (University of Maine), Donald Johnson, Bruce Burtin (Portland Maine Surfcasters Association), and Michael Hogan (Freeport, Maine, Police Dept.).

Special appreciation is extended to Jeremy King for his frequent assistance in the field and to Peter Thayer, Bruce Joule, and Clarisse Simard for their occasional help.

We would also like to thank Gene Letourneau (Waterville, Maine Morning Sentinel) and Bernie Monegain (Brunswick, Maine Times Record) for publicizing our interests on juvenile bluefish, and Robert Nyman (E.P.A., Wash. D.C.), Richard McBride (Rutgers University, New Brunswick, New Jersey) and David Conover (State University of New York, Stony Brook, New York) for sharing their knowledge of mounting, processing, and counting daily growth rings with us and for answering our inquiries. Appreciation is extended to Lila Achor and Laura Livingston for typing this manuscript.

This study was funded through Wallop-Breaux (Federal Aid Project Agreement F-36-R-1).

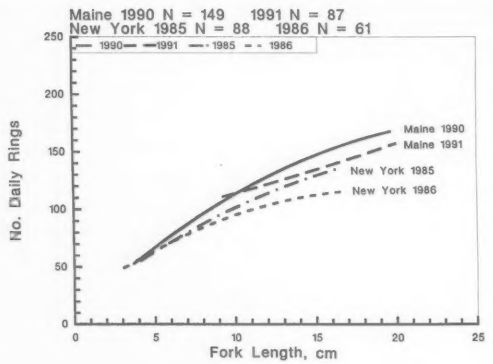


Figure 5

A comparison of the relationship of fork length to number of daily rings for juvenile bluefish, *Pomatomas saltatrix*, from Maine and New York. The regression equations are $Y = 8.53468 + 12.89328X - 0.24416X^2$, $R^2 = 0.847$, for Maine 1990; $Y = 79.49049 + 2.97353X + 0.4563X^2$, $R^2 = 0.635$, for Maine 1991; $Y = 15.19726 + 10.63463X - 0.20203X^2$, $R^2 = 0.840$, for New York 1985; and $Y = 20.22134 + 10.12947X - 0.26495X^2$, $R^2 = 0.835$, for New York 1986.

Literature cited

Baird, S. F.
1873. Condition of the sea fisheries of the south coast of New England in 1871–1872. U.S. Comm. Fish Fisheries. Parts 1 and 2: The bluefish, p. 235–252.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. Fish. Bull. 53:1–577.

Breder, C. M., Jr.
1922. Observations on young bluefish. Copeia 106:33–36.
Briggs, J. C.
1960. Fishes of world-wide (circumtropical) distribution. Copeia 3:171–180.
Bumpus, D. F., and L. M. Lauzier.
1965. Serial atlas of the marine environment. Folio 7: Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Am. Geographical Soc., New York, NY, 23 p.
Chiarella, L. A., and D. O. Conover.
1990. Spawning season and first-year growth of adult bluefish from the New York Bight. Trans. Am. Fish. Soc. 119:455–462.
Clark, J. R.
1973. Bluefish. *In* A. L. Pacheco (ed.), Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic coast estuaries. National Marine Fisheries Service, Middle Atlantic Coast Fisheries Center, Technical Publication 1, Highlands, NJ, p. 250–251.
Collins, M. R., and B. W. Stender.
1987. Larval king mackerel (*Scomberomorus covalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States 1973–1980. Bull. Mar. Sci. 41:822–834.
Creaser, E. P., and D. A. Libby.
1986. Tagging of age 1 herring (*Clupea harengus* L.) and their movement along the Maine and New Brunswick Coasts. J. Northwest Atl. Fish. Sci. 7:43–46.
Deuel, D. G., J. R. Clark, and A. J. Mansueti.
1966. Description of embryonic and early larval stages of bluefish, *Pomatomus saltatrix*. Trans. Am. Fish. Soc. 95:264–271.
Friedland, K. D., G. C. Garman, A. J. Bejda, A. L. Studholme, and B. Olla.
1988. Interannual variation in diet and condition in juvenile bluefish during estuarine residency. Trans. Am. Fish. Soc. 117:474–479.
Grant, C. C.
1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Sci. 3:45–47.
Greeley, J. C.
1939. Fishes and habitat conditions of the shore zone based upon July and August seining investigations. *In* A biological survey of the salt waters of Long Island. 1938. Part II. Suppl. to 28th Ann. Rep. No. XV, New York Cons. Dep., Albany, NY, p. 72–91.
Harden Jones, F.
1968. Fish migration. St. Martin's Press, New York, NY, 325 p.
Herman, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103–109.
Hildebrand, S. F., and W. C. Schroeder.
1928. Fishes of Chesapeake Bay. Bull. Bur. Fisheries 43:231–234.
Hubbs, C. L., and K. F. Lagler.
1958. Fishes of the Great Lakes region. Cranfield Inst. Sci., Bloomfield Hills, MI, 213 p.
Hynes, H. B. N.
1950. The food of fresh water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Animal Ecol. 19:36–58.
Kendall, A. W., and N. A. Naplin.
1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fish. Bull. 79:705–726.
Kendall, A. W., and L. A. Walford.
1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. 77:213–227.
Lassiter, L. L.
1962. Life history aspects of the bluefish, *Pomatomus saltatrix* (Linnaeus) from the coast of North Carolina. M.S. thesis. North Carolina State College, Raleigh, NC, 103 p.
Linton, E. D.
1905. Parasites of fishes of Beaufort, North Carolina. Bull. U.S. Bur. Fish. (1904) 24:321–348.
Lund, W. A.
1961. A racial investigation of the bluefish, *Pomatomus saltatrix* (Linnaeus), of the Atlantic coast of North America. Boletin del Instituto Oceanografico Venezuela 1 (1):73–129.
Lund, W. A., and G. C. Maltezos.
1970. Movements and migrations of the bluefish, *Pomatomus saltatrix*, tagged in waters of New York and southern New England. Trans. Am. Fish. Soc. 99:719–725.
Lyman, H.
1974. Successful bluefishing. Int. Marine Publ. Company, Camden, ME, 22 p.
Morse, W. W., M. P. Fahat, and W. G. Smith.
1987. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1984), Atlas No. 2. Annual distribution patterns of fish larvae. U.S. Dep. Commer., NOAA Tech. Memo NMFS-F/NEC-47, 215 p.
Naughton, S. P., and C. H. Saloman.
1984. Food of bluefish (*Pomatomus saltatrix*) from the U.S. South Atlantic and Gulf of Mexico. NOAA Tech. Memo NMFS-SEFC-150, 37 p.
Nichols, J. T.
1913. Concerning young bluefish. Trans. Am. Fish. Soc. 43:169–172.
Norcross, J. J., S. L. Richardson, W. H. Massmann, and E. B. Joseph.
1974. Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginia coastal waters. Trans. Am. Fish. Soc. 103:477–497.

Nyman, R. M., and D. O. Conover.
1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. 86:237–250.

Oben, L. C.
1957. About the drifting approach of fingerline bluefish (*Pomatomus saltatrix* (Linnaeus)) to the shores of the Black Sea in the Karadaga region (1947–1954). Karadagskaia Biol. Stn. Tr. (4):155–157.

Olla, B. L., A. L. Studholme, and A. J. Bejda.
1985. Behavior of juvenile bluefish, *Pomatomus saltatrix*, in vertical thermal gradients: influence of season, temperature, acclimation and food. Mar. Ecol. Prog. Series 23:165–177.

Pearson, J. C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Fish. Wildl. Serv., Fish. Bull. 50:79–102.

Perlmutter, A.
1939. An ecological survey of young fish and eggs identified from tow-net collections. Section I. *In* A biological survey of the salt waters of Long Island. 1938. Part I. Suppl. to 28th Ann. Rep. No. XV, New York Conserv. Dep., Albany, NY, p. 11–71.

Pierce, H. D.
1883. The spawning of bluefish and opinion of the cause of mortality of fish in the Gulf of Mexico. Bull. U.S. Fish. Comm. 1882–1883, p. 332–333.

Powles, H.
1981. Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:207–209.

Richards, S. W.
1976. Age, growth, and food of bluefish (*Pomatomus saltatrix*) from east-central Long Island Sound from July through November 1975. Trans. Am. Fish. Soc. 105:523–525.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Greed, and L. Ejsymont.
1984. Spawning strategies of fishes in relation to circulation,phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18:1–19.

Smale, M. J., and H. M. Kok.
1983. The occurrence and feeding of *Pomatomus saltatrix* (elf) and *Lichia amia* (leervis) juveniles in two Cape south coast estuaries. S. Afr. J. Zool. 18:337–342.

deSylva, D. P., F. A. Kalber Jr., and C. N. Shuster Jr.
1962. Fishers and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper waters. Univ. Del. Mar. Lab. Inf. Ser. Publ. 5, 164 p.

Targett, T. E., and J. D. McCleave.
1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Am. Fish. Soc. 103:325–330.

U.S. Department of Commerce.
1990–1991. Tide tables of the east coast of North and South America. U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Rockville, MD.

Wilk, S. J.
1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Sandy Hook, NMFS Tech. Ser. Rep. No. 11, 56 p.

Windell, J. T.
1971. Food analysis and rate digestion. IBP (International Biological Programme) Handbook 3:215–226.

Differences between the sagitta, lapillus, and asteriscus in estimating age and growth in juvenile red drum, *Sciaenops ocellatus*

Andrew W. David
J. Jeffery Isely*
Churchill B. Grimes

Panama City Laboratory, Southeast Fisheries Science Center,
National Marine Fisheries Service, NOAA
3500 Delwood Beach Road, Panama City, Florida 32408

Abstract.—Most red drum, *Sciaenops ocellatus*, age and growth research has utilized sagittal otoliths. We evaluated the other otoliths, the lapilli and asterisci, as well as the sagittae, as ageing structures and length-at-age estimators in hatchery-reared and wild juveniles (<50 mm SL). Our otolith mounting and sectioning protocol for preparing sagittal sections required significantly less processing time with no loss in accuracy than the more traditional transverse sectioning reported in the literature. Increments in asterisci were clearly visible from the primordium to the otolith margin, whereas the nuclear region of sagittae and lapilli were more opaque and prevented detection of all rings. Asterisci were not present at hatching, but on average form six days later, therefore the addition of a constant (6 days) to the ring counts of asterisci resulted in this otolith providing more accurate ages than sagittae or lapilli. According to coefficients of determination (r^2) generated from the relation between fish length and otolith diameter, the sagitta, asteriscus, and lapillus predict fish length in descending order. However, because inner rings on sagittae were usually undetectable, lengths at ages cannot accurately be predicted. All rings are observable in the asteriscus; thus, by using the 6-day adjustment factor accurate length-at-age prediction is possible.

The red drum, *Sciaenops ocellatus*, is a recreationally and commercially important marine fish ranging throughout the Gulf of Mexico and along the Atlantic seaboard to Massachusetts. An estuarine-dependent species, red drum spawn offshore, and juveniles move to estuarine nursery areas. After reaching sexual maturity at about age 5 (Mercer, 1984), these fish migrate offshore, where they aggregate into large schools. Concern for the declining status of the resource has prompted many Gulf of Mexico and Atlantic states to implement research to provide a sound scientific basis for management. This research includes aspects of early life history important to recruitment processes (Holt et al., 1983), age and growth (Peters and McMichael, 1987; Comyns et al., 1989), artificial propagation (Arnold, 1988), behavior (Fuiman and Ottey, 1993), and spawning stock abundance (Comyns et al., 1991).

An overwhelming percentage of age and growth investigations have utilized the sagittae because they are the largest of the three otoliths and therefore the easiest to extract and examine (Irie, 1960; Campana and Neilson, 1985). Since Panella (1971) first identified daily growth increments in sagittal otoliths, the formation of daily rings has been confirmed in many species (Jones, 1986).

References to the lapillus are uncommon in the literature. Bailey and Stehr (1988) reported use of the lapillus to age larval walleye pollock, *Theragra chalcogramma* (Pallas), younger than 20 days because it was larger than the sagitta up to that age. Brothers and McFarland (1981) used lapilli to age juvenile French grunts, *Haemulon flavolineatum*. References to the use of the asteriscus in ageing are unknown.

Previous ages for red drum larvae (Comyns et al., 1989) and juveniles (Peters and McMichael, 1987) were derived from sagittae. Peters and McMichael (1987) found that the inner ring structure was usually unclear in juveniles. They used ten larval otoliths to measure the distance from the primordium to the tenth ring, then began juvenile ring counts with the eleventh ring, 56 µm

Manuscript accepted 22 December 1993.
Fishery Bulletin 92:509–515 (1994).

* Present Address: U.S. Fish and Wildlife Service, South Carolina Cooperative Fish and Wildlife Research Unit, G-08 Lehotsky Hall, Clemson University, Box 340362, Clemson, South Carolina 29634.

from the primordium (the mean distance to the tenth ring from the ten larval otoliths). The juvenile otoliths were transversely sectioned and glycerin-cleared. This method was verified by examination of the innermost rings from exceptionally clear juvenile otoliths.

We examined sagittae, lapilli, and asterisci to determine the best ageing structure for juvenile red drum by comparing ring counts for each otolith with known ages in hatchery-reared fish. We also evaluated the relation between fish length and otolith diameter for use in backcalculating lengths at age from each otolith. We report the size at which otoliths are formed to evaluate possible biases in age estimations.

Materials and methods

Wild-caught and known-age (laboratory-reared) juvenile red drum were preserved in 70% ethanol. Standard lengths of fish were measured to the nearest 0.1 mm prior to the removal of otoliths. We made no attempt to measure shrinkage due to preservation or to adjust our measurements accordingly. Otoliths were extracted between crossed polaroids by using a dissecting microscope at 6–12× magnification and transmitted light. This procedure exploited the birefringence of the crystalline structure of otoliths and greatly aided otolith location and removal. Extraneous tissue was removed, and the otoliths were mounted concave side up on glass slides. Two mounting media were used, thermoplastic cement and a polymer mounting medium. The thermoplastic cement allowed easier otolith manipulation and the polymer provided a less brittle and more transparent mount. Otoliths were ground in the sagittal plane with 600-grit carborundum paper and polished with 0.9-µm aluminum oxide sheets prior to examination under a compound microscope. Otoliths mounted with thermoplastic cement were ground to the primordium, flipped convex side up, and again ground to the primordium. Polymer mounted otoliths were ground to the primordium from the concave side. The polished otoliths were illuminated with plane-polarized transmitted light to optimize ring resolution. Ring counts were determined at 125–250× for sagittae and at 250–500× for lapilli and asterisci. To avoid bias from sequentially ageing all three otoliths from the same fish, all sagittae were aged first, followed by all lapilli and all asterisci. After ageing, mean ring counts, standard deviations, and coefficients of variation were calculated.

Otolith diameters (µm) were measured with a digital image analysis system (Optimas ver 3.01, Bioscan, Edmunds, WA). Otolith diameter was defined as a chord from the anterior rostrum to the posterior edge, passing through the primordium. The relationship between standard length and otolith diameter was examined by plotting otolith diameter on standard length and calculating the regression.

We examined larvae and juveniles to determine the size at which otoliths were formed. Larvae were translucent under transmitted polarized light, so otoliths were observable without dissection in fish as small as 4.0 mm SL. To precisely determine fish size at asteriscus formation, five larvae between 2.7 and 3.5 mm SL were dissected and the disrupted otic capsules mounted on glass slides with polymer mounting medium and examined microscopically.

Results

Wild-caught fish ranged from 15 to 50 mm SL, and laboratory-reared fish ranged from 18 to 25 mm SL. Fifty laboratory-reared and 70 wild-caught juveniles were processed; six otoliths were removed from each fish. The sagittae were used as landmarks to locate the smaller lapilli and asterisci. The lapilli were anterior and distal to the sagittae, and the asterisci were posterior and proximal to the sagittae. The asterisci were often found attached to the saccular tissue removed with the sagittae. To determine the size at otolith formation, we examined 35 wild-caught red drum larvae ranging from 1.3 to 7.0 mm SL. Sagittae and lapilli were present in all larvae examined. Asterisci were found in all dissected fish ≥3.0 mm SL (n=5) and not detected in fish smaller than 2.8 mm SL (n=3). In specimens that were not dissected, asterisci were first observed in larvae 3.8 mm SL and were present in all larvae larger than 4.0 mm SL.

Considerable differences were found in the general size and shape of the otoliths (Fig. 1). All otoliths were spherical or slightly ovoid in larvae ≤5 mm SL. Sagittae in larvae ≥5 mm SL began to develop a rostral process, and sagittae of 10-mm larvae were oval, laterally compressed, and had developed a prominent rostrum. The general shape of sagittae did not change in fish 10–50 mm SL. Lapilli followed the same initial development, but the posterior margin of these otoliths became scalloped when larvae were approximately 15 mm SL owing to the formation of numerous accessory primordia. Initially asterisci were also spherical, but the axis of growth changed, with subsequent development resulting in a kidney-shaped appearance by 15 mm SL. Accessory primordia were seldom observed in sagittae and were not observed in asterisci. Lapilli and asterisci were similar in size; however, the diameter of sagittae was approximately three times larger and grew approximately five times faster than asterisci and lapilli (Fig. 2).

Diameters of asterisci and lapilli were well correlated with standard length, but the strongest relation between otolith diameter and standard length was observed in sagittae (Fig. 2). Anterior rostra and

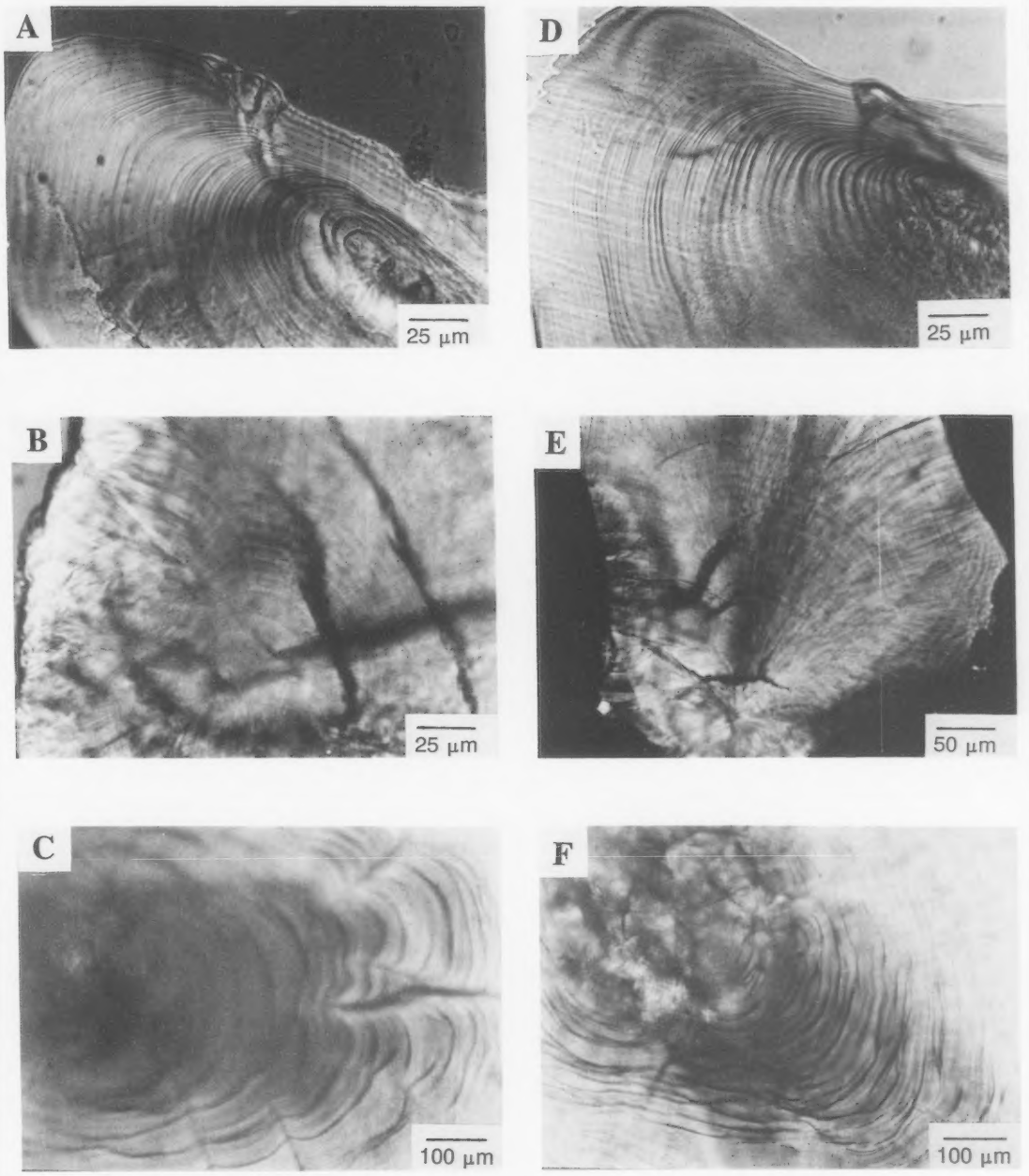


Figure 1

Red drum, *Sciaenops ocellatus*, otoliths: (**A**) hatchery asteriscus 500×; (**B**) hatchery lapillus 500×; (**C**) hatchery sagitta 125×; (**D**) wild asteriscus 500×; (**E**) wild lapillus 250×; (**F**) wild sagitta 125×.

otolith primordia were well defined in sagittae, which, along with a uniform axis of growth, resulted in a more consistent axis of measurement. The lapillus and asteriscus were more circular in shape than the sagitta and had a less well-defined anterior rostrum. The lapillus also formed accessory primordia, which were reflected in an irregular perimeter. Although accessory primordia were not observed in asterisci, the axis of growth shifted with development, resulting in diameter measurements through the primordia that did not necessarily reflect the maximum otolith diameter. These features resulted in greater variability of diameter measurements for asterisci and lapilli than for sagittae.

The accuracy and precision of age estimates varied among otoliths. Fish used to estimate daily ages were collected 46 days after hatching. Although increments were present in all three otoliths, the definition and resolution of the rings differed, especially near the primordia. The mean ring counts, standard deviations, and coefficients of variation are presented in Table 1. All increment widths exceeded the limit of resolution for light microscopy by more than an order of magnitude (Jones and Brothers, 1987; David and Paul, 1989). All ring counts substantially underestimated the age of the 46-day-old hatchery-reared fish. The asteriscus underestimated the true age by 6 days, while sagittae and lapilli underestimated age by 21 days and 25 days, respectively. To obtain realistic age estimates using asterisci, ring counts were adjusted because that otolith is not formed at hatching, but age estimates from ring counts in lapilli and sagittae were erroneously low because all rings could not be observed and counted because of poor contrast in the nuclear region. In addition to providing the most accurate age, coefficients of variation indicated that the asteriscus was also the most precise indicator of true age.

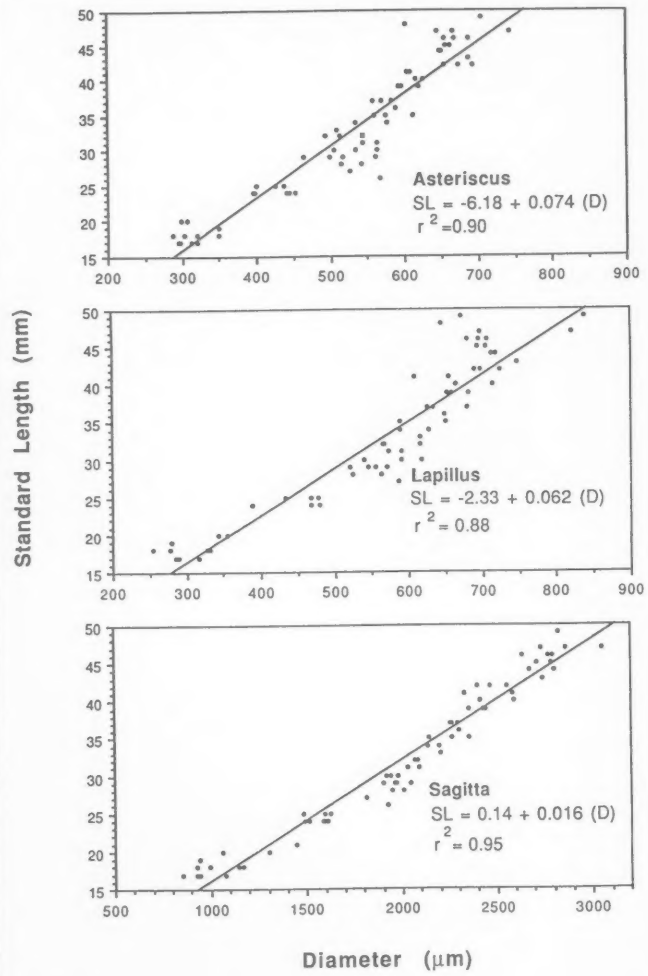


Figure 2

Fish length and otolith diameter relationships for each otolith type of red drum, *Sciaenops ocellatus*. Otolith diameter (μm) plotted on standard length (mm) with linear regression lines overlaid (n=70).

Discussion

Shrinkage of larvae due to preservation has been found to be significant (Blaxter, 1971; Theilacker and Dorsey, 1980; Hay, 1982; Brothers et al., 1983; and Leak, 1986). We did not adjust length measurements for shrinkage due to preservation because most specimens were juveniles (15–50 mm SL), and because we immediately fixed specimens in ethanol which has been shown to minimize the problem of shrinkage (Radke, 1989).

Daily increment formation has been validated in sagittae by using laboratory-reared red drum that were up to 21 days posthatch (Peters and McMichael, 1987). The 6-day underestimate in age determined from the asteriscus of known-age (hatchery-reared) fish corresponded well with age at otolith formation (6–7 days)

Table 1

Comparison of ages derived from sagittal sections of each otolith type in known age (46 days), hatchery-reared red drum, *Sciaenops ocellatus*. Values are reported for mean age, standard deviation, and coefficient of variation.

Otolith	*N*	Mean age (d)	SD	CV
Asteriscus	50	39.7	3.2	8.0
Sagitta	50	25.0	4.6	18.6
Lapillus	50	21.0	5.5	26.3

determined by examination of the age series of larvae, indicating that rings were indeed formed daily, and all rings were visible. Therefore, we assumed that rings were also formed daily in the lapillus and that underestimation of age was due to the inability to observe rings of low contrast in the opaque nuclear area rather than to other possibilities that have been reported, i.e. nondaily ring formation due to poor growth in herring, *Clupea harengus*, and turbot, *Scophthalmus maximus* (Geffen, 1982), and to ring spacing below the resolution limit of light microscopy in striped bass, *Morone saxatilis*, under suboptimal feeding regimes (Jones and Brothers, 1987).

Peters and McMichael (1987) had difficulty distinguishing the innermost rings in sagittae of some juveniles, and they developed an ageing method that did not require counting these rings. This method utilized transverse sections of larval sagittae in which rings were clearly visible to determine the distance from the primordium to the tenth ring. Subsequent juvenile ring counts were initiated at this distance away from the primordium. We also encountered difficulty in detecting all the rings near primordia in sagittae (and lapilli as well) due to the opacity of the nuclear region of the otoliths, but all rings were usually clearly visible in asterisci. Peters and McMichael (1987) made relatively accurate ring counts beyond the tenth ring on sagittae of 21-day-old known-age fish. However, we were not able to duplicate their success using our technique, because our counts underestimated the true age of 46-day-old fish by 21 days with a coefficient of variation of 18.6%. Duplicating their glycerin soaking technique did not improve our ring detection capability. The principle difference between our method and that of Peters and McMichael (1987) was the sectioning plane; they used the transverse plane, whereas we used the sagittal plane.

Because the otoliths were birefringent, they were easily observed within larval fish when illuminated with transmitted light between crossed polaroids. Sagittae and lapilli were easily seen in fish as small as 1.3 mm SL, whereas asterisci were observed in all fish greater than 3.0 mm SL. Comyns et al. (1989) detected two rings in sagittae and lapilli of larvae 2 days after fertilization (1 day posthatch), demonstrating that sagittae and lapilli are present at hatching; according to their growth curve, fish 3.0 mm SL were approximately 6 days old. Whereas the size at hatch was relatively constant, growth varied considerably with temperature, but the variation was not significant until the fish attain 4.0 mm SL (Comyns et al., 1989). Changes in growth rates due to water temperature are therefore not likely to have a significant effect on our estimate of age at asteriscus formation. Others have reported asteriscus formation at similar ages, e.g. at age 6 days in the Japanese eel, *Anguilla japonica* (Umezawa et al., 1989).

The asteriscus provided the most accurate estimate of age for juvenile red drum because it underestimated true age by only 6 days compared with 21 days for the sagitta and 25 days for the lapillus. The asteriscus ages were also the most precise, because the coefficient of variation was only 8.0% compared with 18.6 and 26.3% for the sagitta and lapillus respectively. Most of the variance in age estimates for all three otoliths was caused by the inability to resolve rings near the primordium and at the margin. Rings in the mid portion of asteriscus sections were consistent in shape, increment width, and clarity; a dominant, consistently identifiable, first ring was visible at the edge of the primordium.

The sagitta provided the next most accurate and precise estimates. Ages were underestimated by 21 days on average, and rings near the primordia were difficult to distinguish, resulting in a coefficient of variation more than a factor of two higher than that of the asteriscus. Because sagittae were present at hatching and early rings were detectable in smaller and younger fish (Peters and McMichael, 1987; Comyns et al., 1989), better accuracy and precision of ageing using sagittae may be possible with improvements in preparation and processing of the otolith. However, the Spurr mounting technique (Haake et al., 1982) used by Peters and McMichael (1987) and Comyns et al. (1989) can require several days for proper dehydration, curing, sectioning, and polishing whereas our polymer method required less than one hour to produce ground and polished slides from whole fish, thus allowing considerably more fish to be processed in comparable time periods.

Ages estimated from the lapillus were least accurate and precise because of poor clarity of rings near the primordia and because of the formation and fusion of numerous accessory primordia. This fusion of accessory primordia resulted in superimposition of rings near the margin and the presence of several planes of growth being visible in the same focal plane.

Although additional preparation may have increased resolution of rings near the primordia, poor ring resolution caused by accessory primordia would probably not have been improved.

The addition of a constant to asterisci ring counts (6 days) adjusted for the time lag between hatching and otolith formation and was not used to compensate for uncounted rings. The addition of constants to estimates of age did not affect the rank of the coefficients of variation.

All otolith diameters, especially sagittae, exhibited a strong correlation with fish lengths. This relation can be useful in backcalculating size at age. However, because the ring count did not accurately estimate age, accurate ages derived from sagittae can not be associated with back-calculated sizes. The relation between asteriscus diameter and fish length was not as strong as with sagittae, but the improvements in accuracy and precision in estimating age would increase the confidence in back-calculated sizes at age. However, because asterisci were not present at hatching, size-at-age information for fish <7 days old could not be backcalculated. Rings formed in the asteriscus were concentric and proportionally spaced throughout the otolith because no accessory primordia were formed, making it straightforward to measure radii or increment widths precisely regardless of the chosen axis of measurement.

We conclude that the asteriscus is the best structure to use in ageing young red drum >4.0 mm SL. Using our sagittal section technique with juveniles, we found that the asterisci clearly provided superior accuracy and precision in ageing. Previous efforts by Peters and McMichael (1987) to age juvenile red drum using transverse sections of sagittae provided reasonable age estimates; however, because they began counts a standard distance from the primordium to allow for uncounted rings (10), the accuracy and precision of resulting counts on 21-day-old fish cannot be known in the same sense that we estimated these statistics when all rings were counted on asterisci of 46-day-old fish. The advantage of using asterisci is that clear rings can be seen in sagittal sections, and grinding asterisci in the sagittal plane can be done relatively quickly. Furthermore, all rings were visible in the asteriscus, and only adjustment for age at formation was required to estimate true age.

Literature cited

Arnold, C. R.
1988. Controlled year-round spawning of red drum *Sciaenops ocellatus* in captivity. Contrib. Mar. Sci. Supp. to Vol. 50:65–70.

Bailey, K. M., and C. L. Stehr.
1988. The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 122:147–161.

Blaxter, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 160:128–136.

Brothers, E. B., and W. N. McFarland.
1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts (*Haemulon flavolineatum*). Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 369–374.

Brothers, E. B., E. D. Prince, and D. W. Lee.
1983. Age and growth of young-of-the-year bluefin tuna, *Thunnus thynnus*, from otolith microstructure. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:49–59.

Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 44:1014–1032.

Comyns, B. H., J. Lyczkowski-Shultz, C. F. Rakocinski, and J. P. Steen Jr.
1989. Age and growth of red drum larvae in the North-Central Gulf of Mexico. Trans. Am. Fish. Soc. 118:159–167.

Comyns, B. H., J. Lyczkowski-Shultz, D. E. Neiland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the north-central Gulf of Mexico: seasonality and spawning biomass. *In* R. D. Hoyt (ed.), Larval fish recruitment and research in the Americas: proceedings of the thirteen annual larval fish conference; Merida, Mexico, May 1989, p. 17–26. NOAA Tech. Rep. NMFS 95.

David, A. W., and J. H. Paul.
1989. Enumeration and sizing of aquatic bacteria by use of a silicon-intensified target camera-linked image-analysis system. J. Microbiol. Methods 9(4):257–266.

Fuiman, L. A., and D. R. Ottey.
1993. Temperature effects on spontaneous behavior of larval and juvenile red drum, *Sciaenops ocellatus*, and implications for foraging. Fish. Bull. 91:23–35.

Geffen, A. J.
1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Mar. Biol. 71:317–326.

Haake, P. W., C. A. Wilson, and J. M. Dean.
1982. A technique for the examination of otoliths by SEM with application to larval fishes. *In* C. F. Bryan, J. V. Conner, and F. M. Truesdale (eds.) Proceedings of the fifth annual larval fish conference, p. 12–15. LSU Press, Baton Rouge, LA.

Hay, D. E.
1982. Fixation shrinkage of herring larvae: effects

of salinity, formalin concentration, and other factors. Can. J. Fish. Aquat. Sci. 39:1138–1143.

Holt, S. A., C. L. Kitting, and C. R. Arnold.
1983. Distribution of young red drum among different sea-grass meadows. Trans. Am. Fish. Soc. 112:267–271.

Irie, T.
1960. The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3(1):203–221.

Jones, C.
1986. Determining age of larval fish with the otolith increment technique. Fish. Bull. 84:91–103.

Jones, C., and E. B. Brothers.
1987. Validation of the otolith increment ageing technique for striped bass, *Morone saxatilis*, larvae under suboptimal feeding conditions. Fish. Bull. 85:171–178.

Leak, J. C.
1986. The relationship of standard length and otolith diameter in larval bay anchovy, *Anchoa mitchilli* (Val.): a shrinkage estimator. J. Exp. Mar. Biol. Ecol. 95:167–172.

Mercer, L. P.
1984. A biological and fisheries profile of red drum, *Sciaenops ocellatus*. N.C. Dep. Nat. Res. Comm. Devel., Div. Mar. Fish., Spec. Sci. Rep. 41, 89 p.

Panella, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Washington, D.C.) 173:1124–1127.

Peters, K. M., and R. H. McMichael Jr.
1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 10:92–107.

Radke, R. L.
1989. Larval fish age, growth, and body shrinkage: information available from otoliths. Can. J. Fish. Aquat. Sci. 46:1884–1894.

Theilacker, G. H., and K. Dorsey.
1980. Larval fish diversity, a summary of laboratory and field research. *In* G. D. Sharp (ed.), Workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 105–142. FAO, Intergov. Oceanogr. Comm., Workshop Rep. 28.

Umezawa, A., K. Tsukamoto, O. Tabeta, and H. Yamakawa.
1989. Daily growth increments in the larval otolith of the Japanese eel, *Anguilla japonica*. Jpn. J. Ichthyol. 35(4):440–444.

Reproductive and trophic ecology of the soldierfish *Myripristis amaena* in tropical fisheries

Anderson J. Dee
P.O. Box 1154
Hayward, Wisconsin 54843

James D. Parrish*
National Biological Survey, Hawaii Cooperative Fishery Research Unit
2538 The Mall, University of Hawaii, Honolulu, Hawaii 96822

Abstract.—Squirrelfish of the genus *Myripristis* are valued in small-scale fisheries throughout much of the tropics. The life history and species biology of most of these soldierfishes is poorly known. For the brick soldierfish, *M. amaena*, in Hawaii and Johnston Atoll, we found that sexual maturity for both sexes was reached between 145 and 160 mm standard length at about six years of age — a large fraction of the apparent maximum size and lifespan. Fecundity was relatively low and increased as the fifth power of body weight. Spawning peaked from about early April to early May, and a secondary peak occurred in September. *Myripristis amaena* is a nocturnal predator, feeding mostly on meroplankton, especially brachyuran crab megalops, hermit crab larvae, and shrimps, but also taking a variety of benthic prey. In pristine fish communities, holocentrids were abundant, quantitatively important (often dominant) reef predators and prey. *Myripristis amaena* (and probably other common and important soldierfish) seems to be relatively long lived (at least 14 years), slow growing, and late maturing. The populations suffer considerable natural predation and depend mainly on the largest and oldest fish for reproduction. Heavy, unregulated fishing of these soldierfish, especially at prereproductive size, may severely reduce populations.

Manuscript accepted 30 December 1993.
Fishery Bulletin 92:516–530 (1994).

Soldierfish, Myripristinae, of the squirrelfish family, Holocentridae, occur widely throughout the tropics (Greenfield, 1965, 1968, 1974). They are typically abundant and are an important component of commercial, recreational, and subsistence fisheries in much of the world's tropics. Throughout most of the central and western Pacific Ocean, the brick soldierfish, *Myripristis amaena* (Castlenau), is an important member of this group (Greenfield, 1968). It contributes significantly to fish communities and to fishery catches in shallow reef and rocky habitats. It is particularly important in the recreational fishery at Johnston Atoll (JA), where it is typically the species caught in greatest abundance (Irons et al.[1]). It is also common in catches throughout the Hawaiian archipelago.

Relatively little quantitative information has been published about the life history and biology of species of the genus *Myripristis*, and very little is available about *M. amaena* in particular. Data about diets are available for only a few species of *Myripristis*; for most of these, sample sizes are small (e.g. 14 specimens for *M. amaena*; Hobson, 1974). Results on age and growth from our studies of the JA population of *M. amaena* have been reported (Dee and Radtke, 1989). There have been no thorough published studies of the reproduction of *M. amaena* or closely related species. Because of the wide distribution, considerable abundance, and substantial fishery importance of *M. amaena*, we undertook to describe more fully its food requirements and trophic position in the community and to quantify the reproductive characteristics that affect the dynamics of its populations. The parameters we determined may also provide reasonable first approximations for similar *Myripristis* species that are less well studied. The results will contribute to an informed approach to management of species that are now typically unmanaged and probably overfished in most localities with even moderately dense human populations.

The JA population of *M. amaena* was the major focus of this study for several reasons. Many biological and ecological characteristics of *M. amaena* (e.g. size, morphology, habits, habitat used, fishery value) seem to be representative of a num-

* To whom correspondence should be sent.

[1] Irons, D. K., R. K. Kosaki, and J. D. Parrish. 1990. Johnston Atoll resource survey. Final report of Phase Six (21 July 1989–20 July 1990). Project rep. to U.S. Army Engineer Distsrict, Honolulu, HI, 150 p.

ber of common soldierfish species. Johnston Atoll provided a logistically good base for study, where *M. amaena* was the dominant *Myripristis* species, with populations not seriously depressed by fishing. The species was plentiful and easily collected at many locations throughout the year, and a good range of sizes was readily available. The importance of *M. amaena* in the fishery at JA facilitated collection of specimens and fishery data.

Materials and methods

Specimen collection and handling

Most specimens used in all analyses were taken at Johnston Atoll, a remote, coral-rich, oceanic pinnacle about 1250 km SW of Honolulu (Halstead and Bunker, 1954; Amerson and Shelton, 1976; Randall et al., 1985; Maragos and Jokiel, 1986). Smaller collections were made from a rich, fringing coral reef tract at Puako in South Kohala on the leeward coast of Hawaii Island (Hayes et al., 1982). A few specimens were collected from the almost uninhabited Northwestern Hawaiian Islands (NWHI), primarily from shallow, coralline areas at French Frigate Shoals and Midway (located about 750 and 2000 km, respectively, northwest of Honolulu).

Specimens from all three locations contributed to size–frequency analysis, visual assessment of gonad condition (maturity), and analysis of gut contents. At JA and Puako, gonad weight was taken to determine reproductive season and size at first reproduction; at JA, gonad samples were preserved for histological examination and estimation of fecundity.

Most specimens at all locations were collected from shallow waters (<15 m). The major methods of collection were spearing, bait casting with a line, and some spot applications of ichthyocide. At JA, we collected specimens from several sites inside the lagoon and just outside the barrier reef. Collections and extensive underwater observations were made at frequent intervals between February 1984 and January 1986. Sampling was less intensive in some months because of constraints on travel to JA. At Puako and in the NWHI, specimens were collected rather widely within coralline habitats. At Puako, about half the specimens were collected as quickly as feasible (May–June 1981), once the species was found to be in reproductive season. Other collections there were distributed throughout the year. In the NWHI, specimens were collected in March, April, May, August, and November.

Standard (SL), fork (FL), and total (TL) lengths of all captured specimens were measured to the nearest millimeter, and weights were taken to the nearest 0.1 g. (Appendix A provides functions, fitted by regression, to convert between SL, FL, and TL.) Whole guts and gonads were excised and preserved in 10% buffered formalin for further analysis. Some specimens were frozen whole and stored for some weeks or months before processing.

Source of size–frequency data

At JA, Puako, and the NWHI, length and weight data from all specimens collected for other purposes were available for size-frequency estimation. In addition, at JA, creel census data were obtained from fishermen's catches on many days over the period of study. Fish landed by boat and shore fishermen were examined, and each specimen was measured and weighed as above. These data provided a much larger and possibly more representative sample than our collections alone.

Feeding

The volume of each complete gut specimen was measured by displacement of water before and after the gut was opened and all contents removed. The total volume of contents was determined by difference. All diet items were sorted into systematic categories and identified to the lowest possible taxa. For each prey category, the number of individuals, length, extent of digestion, location in gut, and volume were recorded. Whole reference specimens were used as an aid in identifying prey items and estimating the original size of the prey by comparison of the dimensions of recognizable parts. Volume of remains in each prey category was estimated by displacement of water (Wolfert and Miller, 1978).

A measure of overall importance of each prey category was calculated by using the Index of Relative Importance (IRI), as defined by Pinkas et al. (1971):

$$\text{IRI} = \text{frequency \%} \times (\text{numerical \%} + \text{volume \%}),$$

where frequency % = (the number of guts containing prey of one category divided by the total number of guts that contained any identifiable prey) × 100;

numerical % = (the number of individuals of one prey category divided by the total number of prey individuals found in all the guts) × 100;

and volume % = (the volume of one prey category divided by the total volume of all prey found in the guts) × 100.

Reproduction

Gonads of 430 specimens from JA were visually examined macroscopically and classified (based on their size, color, texture, and morphology) as male, female, immature, or unknown. A subsample of these gonads from specimens collected during probable reproductive and nonreproductive periods was removed, wet weighed to the nearest 0.001 g, and preserved in 70% isopropyl alcohol for further examination. Gonads selected for histology were prepared and embedded by using Kahles solution (Guyer, 1953, p. 236) with a graded series of ethyl alcohol and butyl alcohol dehydration. Embedded subsamples taken from the anterior, middle, and posterior regions of the selected gonads were then sectioned at 5 and 10 µm, mounted on plain microscope slides, and stained by using Delafield hematoxylin and eosin Y techniques (Humason, 1979, p. 112, 119–123).

Size at first reproduction (SFR) was estimated based on visual examination of gonads and by using the gonadosomatic index (GSI), where:

$$GSI = (\text{gonad wet weight/whole body wet weight}) \times 100.$$

The GSI was plotted against SL for male and female *M. amaena* collected from periods during which the species seemed to be reproductively active. A sharp rise in the GSI at some length indicated the SFR. The SFR was also estimated based on histological examination of gonads from specimens collected during the April 1984 spawning peak. Eggs were examined for size and stage of development from sections of 11 females representing a range of sizes. Staging was based on size, morphology, and staining properties of eggs (Khoo, 1978; Wallace and Selman, 1981). Testes from five males were examined histologically for presence of sperm.

Spawning season was estimated by plotting GSI against month of capture for 99 sexually mature males and females (larger than 145 mm SL) collected throughout the sampling period. Histological sections of samples from March, April, May, July, and August 1984 were examined for further validation of reproductive periods.

We did not identify individual clutches of ova in females. Based on the histology, we identified ova ≥0.4 mm on the major axis as being in an advanced stage of yolk development and defined this stage as mature (Table 1, See Fig. 3). Our fecundity value is an estimate of the number of such ova in a female specimen. Ovaries from 12 gravid females collected at JA during the January 1986 spawning peak were used to estimate fecundity. Three 0.02-g aliquots were taken from the midsection of each ovary. All mature ova (≥0.4 mm on the major axis) were counted with the aid of a binocular dissecting microscope. Fecundity, F, was estimated for each female from the formula:

$$F = ((N_1+N_2+N_3)/3) \times (G/A),$$

where N_1, N_2, N_3 = the number of mature ova in each aliquot;

G = total gonad weight (g);
A = weight of a gonad aliquot (0.02 g).

For specimens from Puako, the same procedures were followed except that no histological preparation or examination was done, and ripeness was estimated simply on the basis of visual appearance of

Table 1

Stages of development of oocytes in the brick soldierfish, *Myripristis amaena* (also see Fig 3).

Stage	Oocyte diameter (mm)	Description
oogonia and primary growth	0.01–0.04	scant cytoplasm; centrally located nucleus; single large nucleolus; stains dark red
perinuclear	0.04–0.056	multiple nucleoli around inner side of nuclear membrane; stains dark purple
secondary growth and yolk vesicle	0.056–0.14	clear-staining cortical alveoli begin as ring at cytoplasm periphery, then increase in size and occupy whole cytoplasm
yolk granule	0.14–0.40	true vitellogenesis; red-staining yolk granules begin to form around cytoplasm periphery (early vitellogenesis) then increase in size and occupy whole cytoplasm (late vitellogenesis); zona radiata first appears
maturation	0.40–0.54	yolk granules fuse into yolk "plates" which stain light blue; fusion begins at center and spreads throughout cytoplasm

the gonad and GSI. The SFR, but not spawning season, was estimated quantitatively by using these measures. Egg sizes were not measured, and fecundity was not estimated.

Results

Feeding

Guts from 64 specimens collected at JA at night contained identifiable prey items (Table 2). Crab larvae dominated the diet, producing much larger IRI values than any other major systematic group (Table 3). Brachyuran megalops (mostly Portunidae) were found in over 90% of the analyzed guts. Despite their relatively small size, they were important in volume (28%) as well as numbers (38%). Hermit crab larvae (Paguroidea) were present in over half the guts, and alpheid shrimp in slightly less than half. Both these groups provided significant fractions of all prey numbers and volume and had large IRI values; hermit

Table 2

Diet of *Myripristis amaena* based on 64 specimens from Johnston Atoll, 9 from the Northwestern Hawaiian Islands, and 22 from Puako, Hawaii Island. Results reported by Hobson (1974) based on 14 specimens from Kona, Hawaii Island, are also included for comparison. Table shows the percent of predator individuals that consumed each prey (F), and the percent of all numbers (N) and volume (V) provided by each prey. Values for the highest systematic levels are printed in bold. (See Table 3 for Indices of Relative Importance for these highest level groups.)

	Numerical percent[1]			Volume percent[1]				Frequency percent			
						Hawaii Island				Hawaii Island	
Prey category	Johnston Atoll	N.W. Hawaiian Islands	Puako (Hawaii Island)	Johnston Atoll	N.W. Hawaiian Islands	Puako	Kona[2]	Johnston Atoll	N.W. Hawaiian Islands	Puako	Kona[2]
Crabs[3]	**60.8**	**33.3**	**71.2**	**50.3**	**8.4**	**35.0**	**75.1**	**100**	**11.1**	**68.2**	**100.0**
Portunidae	37.8			27.6				90.6			
Paguroidea (hermit crab)	23.0		0.3	22.7		[4]		59.4		4.6	
Galatheidae			8.5			7.7				4.6	
Shrimp	**11.8**	**22.2**	**11.4**	**10.8**	**8.4**	**>2.0**	**9.3**	**46.9**	**11.1**	**27.3**	**28.6**
Alpheidae	11.8		3.5	10.8		0.4		46.9		13.6	
Palaemonidae			2.0			0.6				13.6	
Hippolytidae			3.0			>0.8				13.6	
Caridea unidentified			0.6			[4]				4.6	
Shrimp larvae			0.9			[4]				4.6	
Shrimp unidentified			1.5			0.2				4.6	
Stomatopods	**1.6**	**11.1**	**4.1**	**6.7**	**8.4**	**6.5**	**0.1**	**37.5**	**11.1**	**22.7**	**7.1**
Lobsters	**0.06**		**0.9**	[4]		**21.5**		**3.1**		**13.6**	
Polychaetes	**12.0**		**0.3**	**15.3**		**0.4**	**0.4**	**70[5]**		**4.6**	**7.1**
Eunicidae	6.7			11.7				60[5]			
Nematonereis sp.	6.3			2.8				59.4			
Eunice sp.	0.4			8.9				9.4			
Opheliidae (*Polyophthalmus* sp.)	5.3			3.6				43.8			
Fish	**2.4**	**33.3**	**1.8**	**10.5**	**33.6**	**5.8**	**2.9**	**32[5]**	**22.2**	**22.7**	**21.4**
Eels, unidentified	2.2			8.5				21.9			
Mysids	**5.9**		**0.3**	**4.3**		[4]	**0.3**	**18.8**		**4.6**	**28.6**
Amphipods	**0.1**		**5.0**	**0.1**		**>0.2**	**0.2**	**9.4**		**18.2**	**7.1**
Gammaridea			4.7			0.2	0.2			13.6	7.1
Tanaids	**5.4**			**2.0**				**50.0**			
Copepods			**1.2**			[4]	**0.1**			**9.1**	**7.1**
Isopods							**0.1**				**7.1**
Cephalopods			**0.3**			**1.5**	**1.4**			**4.6**	**7.1**
Octopus sp.			0.3			1.5				4.6	
Gastropods			**3.5**			**1.4**	**0.4**			**22.7**	**14.3**
Crustacean parts, unidentified		[6]	[6]		**41.2**	**25.8**	**9.7**		**66.7**	**77.3**	**57.1**

[1] Data for unidentified crustacean parts are excluded from the calculation.
[2] Data from Hobson (1974); numerical percents were not reported.
[3] Larvae (mostly megalops), except those from the Northwestern Hawaiian Islands that were juvenile majids.
[4] Data are missing.
[5] Calculated from a subset of 31 specimens.
[6] Not countable.

Table 3

Summary of the diet of *Myripristis amaena* at the highest systematic levels of prey. Results are shown as percents of the summed Index of Relative Importance (IRI). (See Table 2 for details at these and other systematic levels.)

Prey category	Johnston Atoll (n=64)	Northwestern Hawaiian Islands (n=9)	Puako (Hawaii Island) (n=22)
Crabs	72.3	18.5	84.8
Shrimp	6.9	13.6	4.3
Stomatopods	2.0	8.6	2.8
Lobsters	[1]		3.6
Polychaetes	12.4		0.04
Fish	2.7	59.3	2.0
Mysids	1.2		[1]
Amphipods	0.01		1.1
Tanaids	2.4		
Cephalopods			0.1
Gastropods			1.3
Crustacean parts, unidentified	Few[2]	Very many[2]	Very many[2]

[1] Data are missing.
[2] Not countable; not included in computation of IRI.

crabs were more important by all measures. Two *M. amaena* specimens contained a total of three lobsters. Fish were moderately important prey by frequency and volume. Many prey specimens appeared to be eels, probably mostly ophichthids. Polychaetes were the most important benthic prey, present in about 70% of all fish and providing over 10% of all prey by numbers and volume.

Twenty-two specimens from Puako contained prey identifiable to some level (Table 2). Nearly 70% of these contained crab megalops larvae; a hermit crab was identified in one of these and a galatheid crab, *Galathea spinosorostris*, in another. Crab larvae were also the major prey in numbers (over 70%) and volume (35%) and were strongly dominant in the IRI (Table 3.). Shrimp were eaten by the second largest number of fish (nearly 30%) and were second in importance numerically (over 10%), but minor in volume. They were far less an important prey at Puako than at JA, and were more evenly divided among Alpheidae, Palaemonidae, and Hippolytidae (including two *Saron marmoratus*). Lobsters (three individuals) appeared in only three guts (14%), but they accounted for over 20% of total prey volume. Both the slipper lobster, *Scyllarides squammosus,* and the Hawaiian clawed lobster, *Enoplometopus occidentalis,* were eaten. No other groups made major individual contributions to the diet. However, stomatopods and fish accounted for at least several percent of the number of consumers (frequency %) and volume. One octopus appeared in the diet at Puako. Benthic prey included at least a few percent gastropods (by the various measures) and a polychaete specimen. Nearly 80% of all fish also contained some quantity of unidentifiable crustacean parts, which accounted for over 25% of the total prey volume. Calculated as a percent of only the total prey identifiable to more specific groups, the volume % of each of those groups was considerably higher.

Only nine specimens from the NWHI contained prey identifiable to any level (Table 2). The total amount of prey recovered was small. Fish (including at least one pomacentrid), shrimp, juvenile crabs (including majids), and stomatopods were found in one or two guts each in total numbers of one to three individuals each. Six guts contained unidentifiable crustacean parts, which accounted for over 40% of the total diet volume. Fish were next in volume, and the other three groups contributed little volume.

At all three locations, the diet of *M. amaena* was heavily dominated by small juvenile stages of crustacean species that become much larger as adults. These prey included all the major groups of large crustaceans that are dominant in the diets of many demersal species of reef fishes studied in Hawaii (Parrish et al., 1985). Besides the crab and shrimp prey — quantitatively important in the diet of *M. amaena* at all three locations — stomatopods were eaten at all locations, and were the dominant prey of the Myripristinae generally in the NWHI (Parrish, unpubl. data). *Pseudosquilla oculata* was a stomatopod species identified in our *M. amaena* specimens that also was prominent in the diets of other Myripristinae and other demersal reef fishes in our studies in Hawaii.

Small peracaridan crustaceans were conspicuous in the diet at JA (Table 2). Mysids and tanaids were present in the gut contents of many fish specimens, and each group contributed a few percent of the total number and volume of prey. Only one individual of each was identified at Puako. Amphipods were somewhat less widely found as diet components at JA and their abundance was trivial. At Puako they were present in about 18% of the fish and made up about 5% of numbers but were trivial in volume. Most of those identified were gammarids. A few isopods were found in JA specimens, and traces of copepods were found in Puako specimens. More peracaridans and other small crustaceans were very likely part of the residue of unidentifiable crustacean parts that appeared widely at all locations.

Myripristis amaena showed the expected strongly nocturnal feeding habit. At JA, guts from all 64 speci-

mens taken between 2000 and 0200 hours contained identifiable prey items. From 62 guts collected in the daytime, only four (taken at 0730 hours) contained more than one identifiable food item. At Puako, all 11 guts collected between 2300 and 0930 hours contained identifiable prey items, all of which might reasonably be the result of night or dawn feeding. Eleven specimens taken between 1000 and 1300 hours contained some food, much of it only unidentified crustacean parts. Sixteen specimens collected between 1100 and 1500 hours contained no identifiable prey. Of 61 specimens from the NWHI, only nine (collected between 0800 and 1100 hours) contained identifiable prey, mostly considerably digested. The remaining 52 specimens, collected between 1000 and 1600 hours, were empty or contained well digested, unidentifiable material.

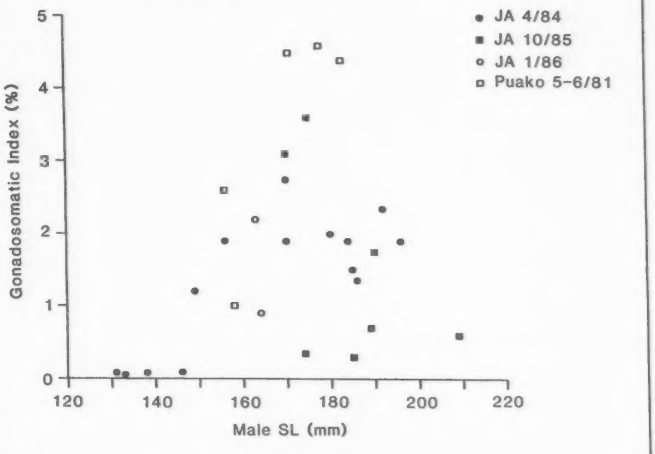


Figure 2

Values of gonadosomatic index and corresponding standard length for male brick soldierfish, *Myripristis amaena*, collected during reproductive peaks at Johnston Atoll (JA) and Puako, Hawaii.

Reproduction

The GSI of each sex collected during reproductive periods throughout the year from JA and Puako combined indicated an increase in the range of 153–156 mm SL for females (Fig. 1) and in the range of 149–156 mm SL for males (Fig. 2). Based on histological examination of developing oocytes in JA females, five developmental stages were identified (Table 1). Sexual maturity was defined based on the presence of ovaries with oocytes in the late yolk granule stage for females (≥0.4 mm diameter; see Fig. 3) and on the presence of mature sperm in males (Fig. 4). The 11 ovaries and five testes examined histologically indicated that first sexual maturity occurred near 154 mm SL for females and 149 mm SL for males. The results were consistent with those from visual examination of 24 total gonads (males and females) from Puako.

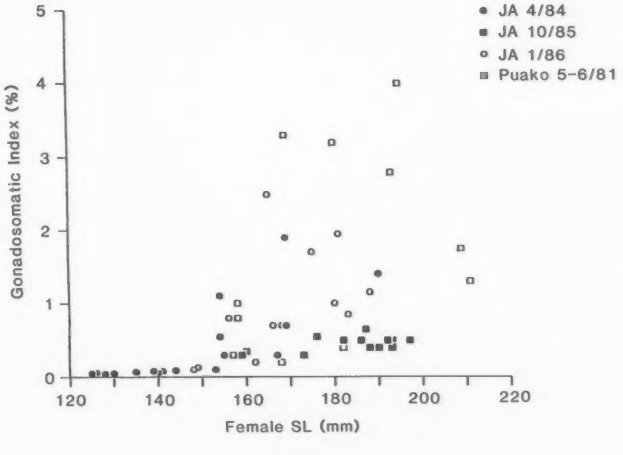


Figure 1

Values of gonadosomatic index and corresponding standard length for female brick soldierfish, *Myripristis amaena*, collected during reproductive peaks at Johnston Atoll (JA) and Puako, Hawaii.

When GSI of mature specimens (larger than 145 mm SL) from JA was plotted against month of capture, with data from all months except September, spawning peaks were discernible in January, April, May, and October; the major peak was in April (Fig. 5). Based on visual examination, GSI, and histology, no gravid individuals were recorded among specimens collected during any other month. (Samples were rather small in some months.)

The fecundity estimated from the 12 ovaries sampled at JA ranged from 12,400 mature ova for a 156-mm SL fish to 69,200 for a 181-mm SL fish (Appendix B). Regressions were performed with fecundity, F, in number of mature eggs as a function of standard length, SL, in millimeters, and alternatively as a function of whole wet body weight, W, in grams. The fit was

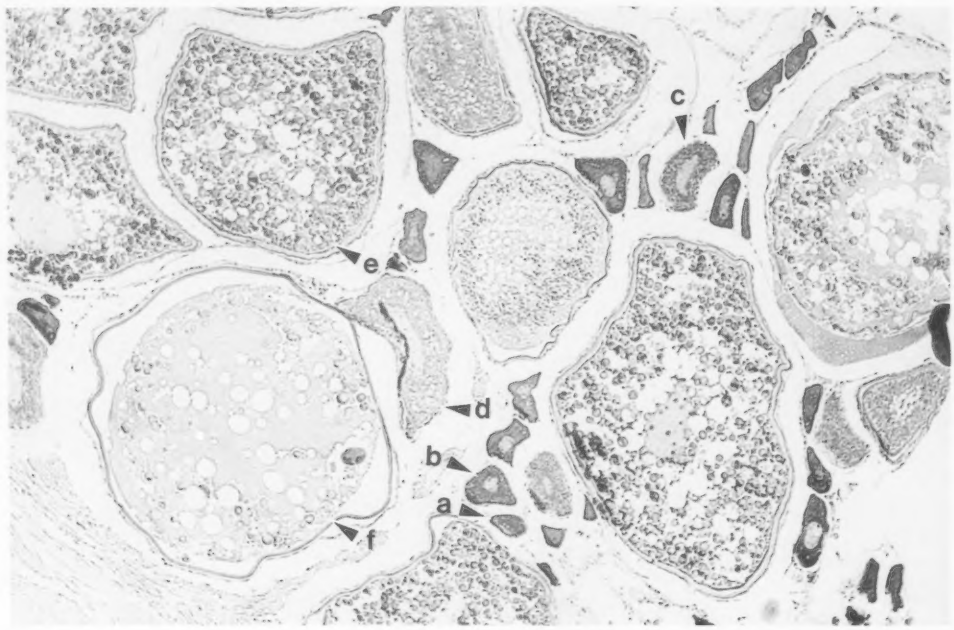


Figure 3

Light micrograph of a section of ovary from a brick soldierfish, *Myripristis amaena*, showing oocyte development stages: (**a**) primary growth, (**b**) perinuclear, (**c**) early yolk vesicle, (**d**) late yolk vesicle, (**e**) yolk granule, and (**f**) maturation.

slightly better for power functions than for linear functions in both cases:

$$F = 5.029 \times 10^{-20}(\mathrm{SL})^{10.614}, \quad r^2 = 0.75$$
$$F = 1.447 \times 10^{-7}\, W^{5.0038}, \quad r^2 = 0.86 \quad \text{(Fig. 6).}$$

Based on the weight-frequency distribution of the recreational catch sampled at JA (Fig. 7A) and our weight-fecundity expression, in an average year, the reproductive output of the population is distributed as shown in Figure 7C. Thus, for example, about 54% of all eggs are produced by fish of 250 g and larger (over 13 years old) — the oldest 20% of the population. Weight classes between 200 and 250 g (ages of about 10 to 13 years) constitute about 38% of the reproductive population and produce about 35% of all eggs. Smaller fish — over 41% of the reproductive population — produce only about 11% of all eggs. Fishing pressure (all recreational) is light at JA, and many large fish remain.

Discussion

Feeding

With the possible exception of some of the larger shrimp and stomatopod specimens, the dominant prey found in our *M. amaena* samples at all three locations were in some sense planktonic. The large number of crab, shrimp, and stomatopod larvae eaten, as well as the presence of prey such as copepods and mysids, strongly indicates that *M. amaena* does much of its feeding in the water column. Hobson (1974) found generally the same prey groups dominant and concluded that *M. amaena*, *M. berndti*, and *M. kuntee* were planktivores at Kona on Hawaii Island. A similar suite of prey items found in *M. kuntee* at Puako in the present work and at Oahu (Oda and Parrish, 1982) indicated that zooplankton were the dominant food source. Our diet studies of *M. berndti* at Puako show a similar result. Brecknock (1969) found that *M. berndti* was primarily zooplanktivorous at Oahu. The results of Harmelin-Vivien (1979) for *M. bowditchae* in Madagascar and of ter Kuile (1987) for *M. murdjan* in the Flores Sea indicate a large proportion of meroplanktonic prey in the diets. These soldierfishes seem morphologically adapted for picking small prey individuals from the water column (Hobson, 1972, 1974), and they have often been observed foraging extensively well above the bottom (Brecknock, 1969; Hobson, 1972, 1974).

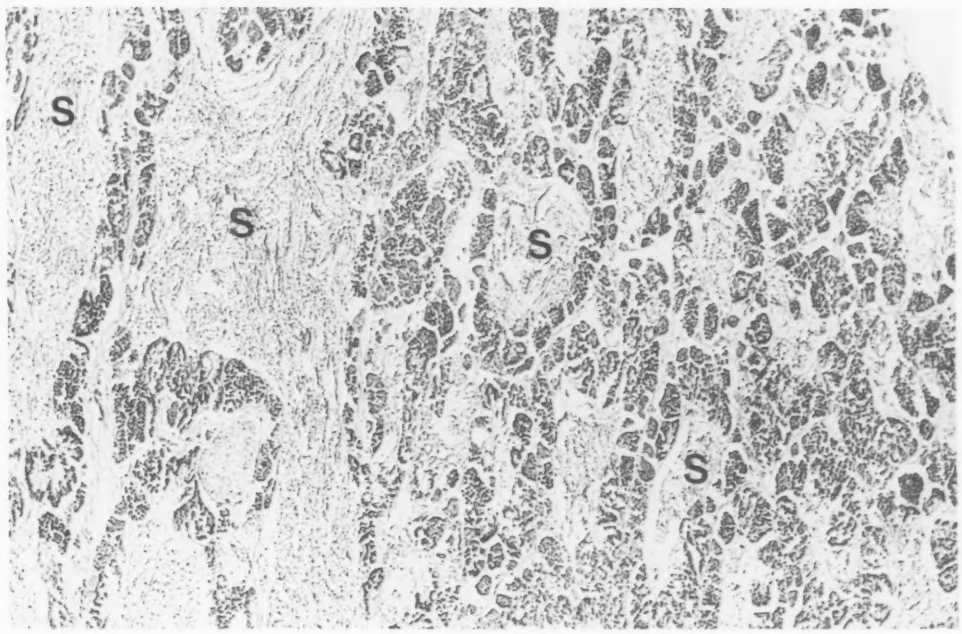


Figure 4

Light micrograph of a section of testis from a brick soldierfish, *Myripristis amaena*. (S) indicates large pockets of mature sperm.

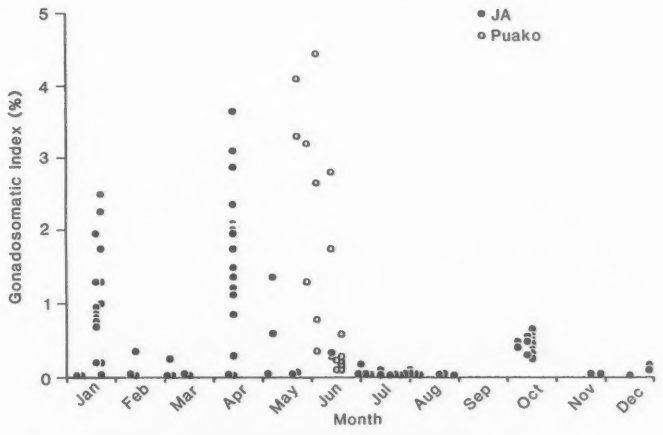


Figure 5

Values of gonadosomatic index and corresponding dates of capture for brick soldierfish, *Myripristis amaena*, collected at Johnston Atoll (JA) and Puako, Hawaii.

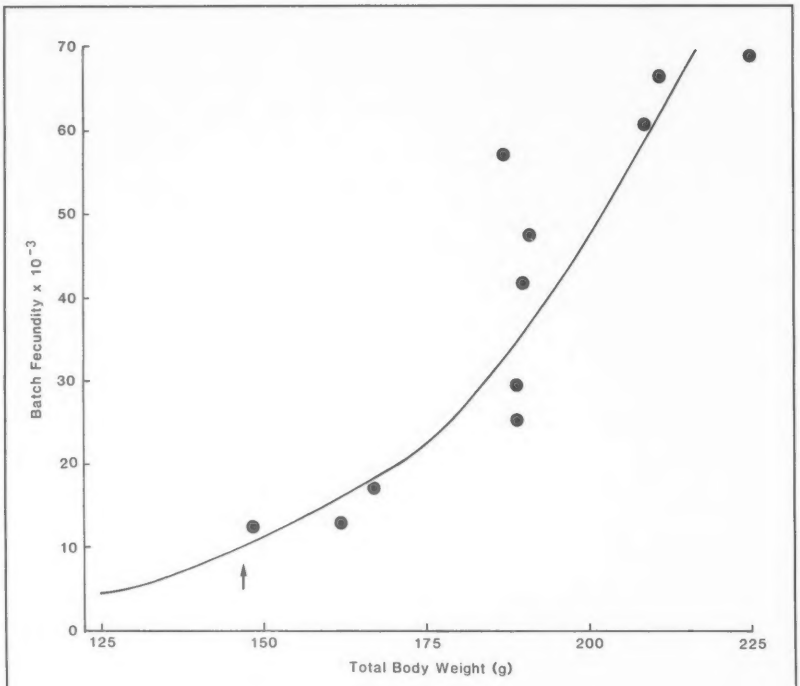


Figure 6

Batch fecundity estimate, F, and corresponding wet body weight, W, for ovaries of 12 brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA). The curve for the functional relationship fitted by regression is shown: $F = 1.447 \times 10^{-7}\ W^{5.0038}$.

A large fraction of all food eaten by *M. amaena* and most other *Myripristis* species appears to be taken from the water column, often at some distance above the substrate. However, relatively little of what we found or of what has been reported in the diets of these species in Hawaii appears to be holoplanktonic. Among the many small crustacean groups identified in the diets, few copepods were found. A number of the common crustacean prey were from groups such as mysids and amphipods that migrate vertically (often on a diel schedule) within shallow water, and may shelter on or near benthic substrate, within caves, cavities, rubble, or other cover during part of the day. Larval and young juvenile forms of larger benthic crustacea, such as crabs, lobsters, stomatopods, and some shrimp, may be components of this migrating "semiplankton." Some shrimps may be intermittently sedentary or free swimming as adults. What is known of this semiplankton (Alldredge and King, 1977; Porter and Porter, 1977; Parrish, 1989) and of the diet and feeding of *Myripristis* suggests that these squirrelfishes are not restricted to either planktonic or benthic feeding, but that they consume these prey groups wherever they are accessible.

The dominance of this semiplanktonic, probably vertically migrating, fauna in the diet of these fishes has important implications for their trophic linkage to the surrounding systems. Whatever the spatial and temporal details of their residence in the water column, the dominant "zooplankton" seem characteristic of an inshore aggregation, probably tied closely to shallow water. Therefore, these squirrelfishes depend for their trophic support largely on local sources of secondary production and possibly even primary nutrients (Parrish, 1989). This trophic arrangement is in contrast to the traditional concept of shallow-water planktivorous fishes supported by holoplankton of open ocean origin brought to the coast by prevailing oceanic currents.

There are reports of some *Myripristis* species feeding close over the substrate (Brecknock, 1969; ter Kuile, 1989). Hiatt and Strasburg (1960) noted that *M. microphthalmus* (=*violaceus*; Greenfield, 1974) in the Marshall Islands "takes a great variety of crustaceans which are associated with, or swim near, the coral mounds in which this...fish secludes itself." They also found that some of their specimens had eaten tube-dwelling polychaetes—clearly a benthic

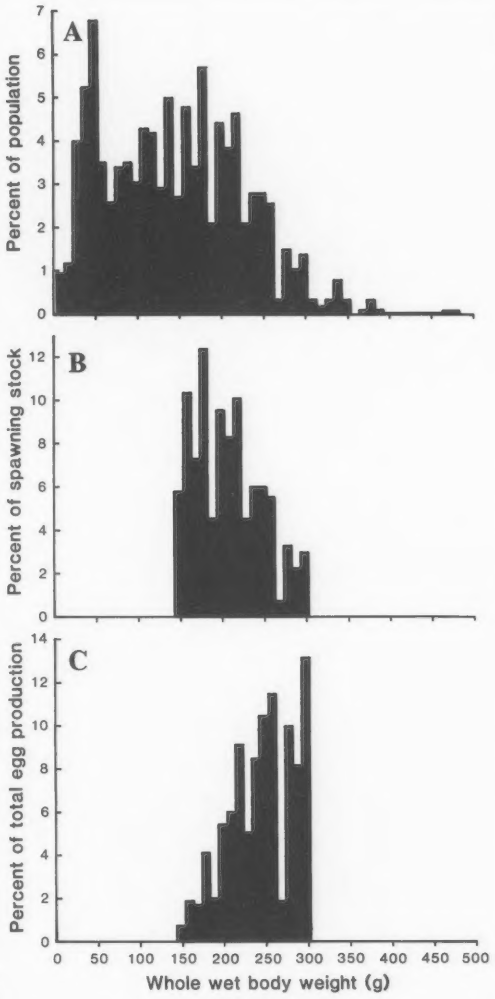


Figure 7

Size-frequency distribution of population numbers and population egg production of the brick soldierfish, *Myripristis amaena*, at Johnston Atoll (JA). (**A**) Distribution of whole wet body weights of all 855 specimens measured from recreational catches and scientific collections combined. (**B**) Distribution of wet weights of only the reproductively mature portion of the population up to 300 g (n=396). (**C**) Distribution of egg production by wet weight of spawners (n=396) based on the spawning population distribution in (B) and the fecundity vs body weight relationship developed from gonad samples. The fish population is arbitrarily truncated at 300 g for (B) and (C), which excludes 25 specimens distributed very irregularly over 18 weight classes, and with sizes much larger than those used to develop the size-fecundity relationship.

prey that was common in adjacent sandy patches. Harmelin-Vivien (1979) reported that polychaetes were the major prey by weight found in *M. bowditchae* (=*murdjan*; Randall and Gueze, 1981) in Madagascar, and she specifically noted that this fish sometimes fed on the bottom. Polychaetes were a minor prey of *M. berndti* at Oahu (Brecknock, 1969) and were fairly abundant in *M. murdjan* in the Flores Sea (ter Kuile, 1989). A polychaete was found in a *M. amaena* specimen from Kona (Hobson, 1974) and in one from our collections at Puako. In our JA collections, they were much more common and abundant, producing the second largest IRI value of the major systematic groups (Table 3). The JA taxa were Sedentaria, which must certainly have been benthic dwellers. At Puako, at least five of our 36 specimens of *M. berndti* and two of our 21 specimens of *M. kuntee* with prey contained polychaetes. Three specimens of *M. berndti* contained several polychaete individuals each.

Gastropods (presumably benthic species) were reported by Hobson (1974) in the diets of *M. amaena* and *M. berndti* from Kona. A benthic gastropod was found in the gut of a *M. berndti* at Puako, and they were fairly common in our *M. amaena* specimens there. Brecknock (1969) found a few gastropods in guts of *M. berndti* from Oahu and reported foraging by this species on the bottom of aquaria. One *M. berndti* specimen from Puako contained part of an arm of a bottom-living ophiuroid.

It seems clear that *M. amaena* and some other *Myripristis* species eat some fully benthic taxa. It is unlikely that such prey make up a major part of the diet for more than a very few *Myripristis* species. However, the ability of these squirrelfishes to employ this feeding mode enables them to exploit a greater range of food resources, at least on an opportunistic basis. Again, the trophic source seems to be local.

Trophic role of squirrelfishes in tropical communities

Holocentrids commonly make up a significant portion of the total natural fish community and are important predators throughout their range. In the uninhabited NWHI, nine species of holocentrids, including *M. amaena*, made up 4.5% of all individuals in the fish community (Norris and Parrish, 1988). In Tulear, Madagascar, three species of holocentrids represented 2.2% of the total fish population (Harmelin-Vivien, 1981). At JA, *M. amaena* alone provided about 2% of all individuals in the fish community. Together with three other species of holocentrids, it accounted for about 3% of the total fish community there (Dee et al.[2]).

[2] Dee, A. J., D. K. Irons, and J. D. Parrish. 1985. Johnston Atoll resource survey; a final report of the initial phase (19 Jan 1984–20 Jul 1985). Project report to U.S. Army Engineer District, Honolulu, 70 p.

The importance of holocentrids as predators has been well documented (Randall, 1967; Hobson, 1974; Vivien and Peyrot-Clausade, 1974; Gladfelter and Johnson, 1983). Gladfelter and Johnson (1983) found that seven species of squirrelfishes made up >99% of the nocturnally active, benthic crustacean-feeding fishes at St. Croix, U.S. Virgin Islands. Randall (1967) reported that holocentrids accounted for about 14% by number and 11% by weight of all zooplankton consumed as prey by the fish community at St. John, U.S. Virgin Islands. In the NWHI, holocentrids, including *M. amaena*, are among the most successful families of fish predators. Holocentrids accounted for nearly 40% by number, over 60% by weight, and about 50% by volume of the large crustacean community (crabs, shrimps, stomatopods, and lobsters) taken as prey by the 78 fish species from 28 families that contained large crustacean prey in our NWHI diet studies. Holocentrids also were responsible for about 2.5% of all the individual fish eaten. The fraction of the complete food consumption (all prey in the community combined) by this entire fish community that is eaten by holocentrids was about 13–17% (Parrish, unpubl. data).

Holocentrids also are an important element of the community as prey for other fishes. In the NWHI, 4% of all identified fish prey individuals were holocentrids (Norris and Parrish, 1988). In the western Atlantic, Randall (1967) found evidence that seven species of fishes from four families had eaten holocentrids; three species from three families had eaten Myripristinae (*Myripristis jacobus*). Dragovich (1970) also found that postlarval holocentrids (including Myripristinae) were fairly common prey of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in the western Atlantic. As a widespread and abundant group that is an active predator and vulnerable prey, holocentrids play a major role in the trophic structure of tropical marine ecosystems.

Reproduction

For specimens from JA, the results from the three independent analyses of gonads (histology, GSI, and visual examination) indicated that sexual maturity of *M. amaena* occurs at 153–156 mm SL for females and at 149–156 mm SL for males. These results correspond closely to SFR estimates from our specimens collected at Puako: 145–160 mm SL, sexes combined (Hayes et al., 1982). Data from both locations are included in Figures 1 and 2. These values of SFR correspond to about 75–80% of L_∞ (as determined by fitting data from length measurements and otolith increment counts to a von Bertalanffy growth model) and to an age of about six years (Fig. 8 in Dee and Radtke, 1989). Dee and Radtke (1989) aged specimens up to nearly 14 years old. Their oldest specimen (of many available for analysis) was somewhat larger than the L_∞ derived from the regression, so it seems unlikely that many individuals live much longer. Therefore, the age at first reproduction (AFR) is probably about 40% (or a little less) of the maximum lifespan commonly attained, and some individuals may reproduce for as many as eight years.

The relation between SFR and maximum body size has been investigated by several workers in a number of locations. The only results reported for squirrelfishes are estimates, based on large sample sizes, for two species of Holocentrinae from the Caribbean Sea (Wyatt, 1976). For *Holocentrus adscensionis*, FL at sexual maturity was about 175 mm, asymptotic (maximum) FL about 265 mm, and the ratio about 0.66; for *Holocentrus rufus*, FL at sexual maturity was about 130–135 mm, asymptotic FL about 230 mm, and the ratio about 0.59. Both these species reach considerably larger sizes than *M. amaena*, and *M. amaena* has the largest SFR/L_∞ ratio of the three species. The ratios for these squirrelfishes seem to be in the high portion of the range of published values for tropical fishes (Munro, 1974; Loubens, 1980). *Myripristis amaena*, in particular, matures at an advanced absolute age and at a surprisingly large fraction of its maximum age and size.

Spawning of *M. amaena* at JA seems to occur primarily in April–May; a secondary peak probably takes place in late September. All specimens collected during the fall peak showed GSI values above the inactive (off-season) level, but considerably below the mean value for the spring peak (Fig. 5). Although no collections were possible in September, visual examination and GSI data from collections made throughout October 1985 suggested the late stages of a spawning period that probably peaked in late September. Back calculation using the total number of otolith increments counted for the two smallest individuals aged by scanning electron microscope examination (Dee and Radtke, 1989) indicated that one individual was spawned in late September and the other in early October. A spawning peak also was observed in specimens collected in January 1986, but not in January 1985. The 1986 event may have resulted from unseasonably calm conditions that occurred during that period. Spawning also was recorded during January 1986 for *Chaetodon trifascialis*, an unusual time of year for that species. Values of the GSI for *M. amaena* collected in January 1986 were generally as high as those of specimens collected during the April spawning peak.

Data were not collected at Puako in a way that would permit a comparable assessment of seasonal

distribution of reproduction. Instead, small collections of specimens were made at regular, frequent intervals only long enough to discern a time of active reproduction. At only that time, a large collection of specimens was made quickly to permit estimation of SFR, and seasonal collections were not continued (Hayes et al., 1982). Thus, the Puako results serve only to establish that reproductive development (e.g. GSI, Fig. 5) is high in May and June. Those months probably represent a peak, but the data do not well define its limits or the pattern for the rest of the year. This early summer high at Puako is contiguous with the late spring high at JA.

Many tropical marine species show a collective spring spawning peak and a second peak in fall (Munro et al., 1973; Watson and Leis, 1974; Johannes, 1978; Walsh, 1987). For Hawaiian fishes, the most dominant seasonal spawning pattern, based on numbers of spawning records, is a peak spawning period in about April and May, with a secondary peak in October for some species. Based on numbers of recruitment records, the dominant recruitment period occurs in June and July, and a secondary peak in February and March (Walsh, 1987). Many studies indicate that there can be considerable variability in the timing of recruitment from year to year, and that the timing and intensity may vary at small spatial scales (Victor, 1982; Williams, 1983; Sale, 1985; Schroeder, 1985; Walsh, 1987, Doherty, 1991).

Larval and newly settled *M. amaena* were elusive throughout the present study, and few data could be collected regarding recruitment. The youngest specimen for which we counted short period (apparently daily) increments in otoliths (Dee and Radtke, 1989) showed a discontinuity that probably represented settlement from the plankton. Back calculation based on the number of increments after the assumed settlement mark suggests that the specimen settled in early February. Although our data regarding settlement are minimal, both these and our spawning results are consistent with the above seasonal reproductive periods summarized by Walsh (1987). Walsh suggested that changes in water temperature or photoperiod, or both, are most likely responsible for observed seasonal patterns of spawning and recruitment in Hawaiian reef fishes. For *M. amaena* at JA, there was no indication that water temperature affected the time of spawning. The full annual range of temperature is very small (24.5–26.5°C). Temperatures during the reproductive period of January 1986 were among the coldest recorded during the entire study, whereas temperatures during spawning in April 1984 were among the highest recorded.

Wyatt (1976) reported on spawning seasons of two Holocentrinae species in Jamaican waters. He recorded ripe *Holocentrus adscensionis* collected in all months except June, and only 2% (one specimen) ripe in July. Most spawning occurred in January, February, and March, but October was also a peak month. Besides ripe fish, "sexually active" gonads were common (14–37% of all gonads) in September through May. The seasonal pattern was similar for *H. rufus*; highest peaks of ripe gonads occurred in October (44%) and February (32%). "Sexually active" gonads were found in all months except July. May, June, and July were the months of lowest gonad development. In Bermuda (15° farther north in mid-ocean), Winn et al. (1964) reported breeding by both these Holocentrinae species in June, July, and August. Variability in timing of spawning due to factors such as lunar periodicity, water temperature, plankton productivity, photoperiod, currents, and rainfall occurs commonly, and spawning time can vary from year to year, even at the same location (Watson and Leis, 1974; Wyrtki, 1974; Johannes, 1978; Walsh, 1987).

The fecundity of *M. amaena* is relatively low compared with many marine species. The most fecund specimen examined contained fewer than 70,000 maturation stage eggs, and the length-fecundity function predicts that a specimen of length L_∞ would contain fewer than 100,000 such eggs. Fecundity increases sharply with body size; it rises with the fifth power of weight and more than the tenth power of SL. (The sample size used for the regressions was not large, but the values of r^2 indicate a reasonably good fit.) These changes with size are much greater than those found in many marine species. These results, together with the results for SFR and the oldest specimen aged, indicate that the species matures slowly. With a relatively long life and steeply increasing fecundity, a very large fraction of the reproductive output of the population is provided by old fish.

The number of spawnings per year is unknown. There was no clear evidence in ovaries examined under direct light microscopy or histologically of a distinct series of distinguishable groups of ova in a graded-size sequence that might represent serial batches spawned within a season. However, production of such serial clutches is commonplace in tropical, nearshore fishes. Unless individual females spawn a good many batches (of the full number of maturation stage eggs estimated) within each year, the total or lifetime fecundity of individuals is relatively low compared with many common marine species. For example, an individual maturing at age six and spawning once annually through age 14, according to the body sizes indicated by our von Bertalanffy expression (Dee and Radtke, 1989) and the fecundity indicated by our length-fecundity expression, would produce fewer than 300,000 eggs during such

a reproductive life. Clearly, determination of the number of clutches spawned in a reproductive season is an important subject for research on *M. amaena*.

Most types of fisheries tend to produce higher mortality of older age classes. Certainly this is true of the common spear fisheries for squirrelfish in the tropics, where larger specimens are individually selected. For a species in which sexual maturity and fecundity are related to age (size) as they are in *M. amaena*, this means that substantial fishing pressure applied to the population can severely reduce egg production (see Fig. 7). The risks of recruitment overfishing are therefore especially great, particularly when maturity occurs late enough that fish of prereproductive size are still a desirable catch. The expected trend as fishing pressure on such a stock increases is the appearance of an increasing fraction of prereproductive fish in the catch. At JA, despite low total fishing effort, about 51% of all *M. amaena* in our creel sample of the fishery were prereproductive; in the small-scale, recreational-subsistence fishery at Puako, about 46% were prereproductive (n=24). Near many centers of human population, fishing intensity is much greater, and great declines in populations of soldierfish are unofficially reported. Clearly the life history of *M. amaena*, and perhaps soldierfishes in general, creates high vulnerability to conventional, unregulated fishing. It seems essential that fisheries for such species be managed to conserve the largest, oldest spawners to protect the reproductive potential of the stock.

Acknowledgments

This research received major funding support from the Department of the Army, U.S. Army Engineer District, Fort Shafter, Hawaii, under contract DACA83-84-C-0019. The work at Puako was supported by the Hawaii Department of Land and Natural Resources in collaboration with the U.S. Fish and Wildlife Service, and by a grant from NOAA Office of Sea Grant through the University of Hawaii Sea Grant College Program. The work in the Northwestern Hawaiian Islands was supported similarly in part by Univ. Hawaii Sea Grant under grants from NOAA Office of Sea Grant, Department of Commerce, by Project NI/R-4 and Institutional Grants NA79AA-D-00085 and NA81AA-D-00070. This is Sea Grant Publication UNIHI-SEAGRANT-JC-94-15. The Ocean Resources Branch, State of Hawaii, Department of Business, Economic Development and Tourism, contributed additional funding. Financial and logistic support also were provided by the Hawaii Cooperative Fishery Research Unit, which is jointly supported by the Hawaii Department of Land and Natural Resources, the University of Hawaii, and the National Biological Survey. A number of Fishery Unit research assistants collected much of the data and assisted with the early stages of analysis for Puako and the NWHI. The Defense Nuclear Agency and the staff of its contractor, Holmes and Narver Services Inc., provided invaluable support with facilities, logistics, and technical expertise on Johnston Atoll. The Pacific Islands Office of the U.S. Fish and Wildlife Service provided access to the National Wildlife Refuge property and collaborated in the overall program of research at Johnston Atoll. We are grateful for the help and expertise of Jim Howard, Darby Irons, Ben Leorna, Chuck Madenjian, Charley Myers, Tim Tricas, and Brian Tsukimura. The paper was considerably improved based on review and comments from T.A. Clarke, E.E. DeMartini, D.W. Greenfield, and E.S. Reese. Susan Monden prepared the figures.

Literature cited

Alldredge, A. L., and J. M. King.
1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 41:317–333.

Amerson, A. B., and P. C. Shelton.
1976. The natural history of Johnston Atoll, central Pacific Ocean. Atoll Res. Bull. 192:1–479.

Brecknock, E. L.
1969. Some aspects of the ecology of *Myripristis murdjan* in the Hawaiian Islands. M.S. thesis, Univ. Hawaii, Honolulu, 22 p.

Dee, A. J., and R. L. Radtke.
1989. Age and growth of the brick soldierfish, *Myripristis amaena*. Coral Reefs 8:79–85.

Doherty, P. J.
1991. Spatial and temporal patterns in recruitment. *In* P. F. Sale (ed.), The ecology of fishes on coral reefs. Academic Press, San Diego, 754 p.

Dragovich, A.
1970. The food of the skipjack and yellowfin tunas in the Atlantic Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 68:445–460.

Gladfelter, W. B., and W. S. Johnson.
1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). Ecology 64:552–563.

Greenfield, D. W.
1965. Systematics and zoogeography of *Myripristis* in the eastern tropical Pacific. Calif. Fish Game 51:229–247.
1968. The zoogeography of *Myripristis* (Pisces: Holocentridae). Syst. Zool. 17:76–87.

1974. A revision of the squirrelfish genus *Myripristis* Cuvier (Pisces: Holocentridae). Los Angel. Cty. Mus. Sci. Bull. 19:1–54.

Guyer, M. F.
1953. Animal micrology, 5th ed. Univ. Chicago, 327 p.

Halstead, B. W., and N. C. Bunker.
1954. A survey of the poisonous fishes of Johnston Island. Zoologica (N.Y.) 39:61–77.

Harmelin-Vivien, M. L.
1979. Ichtyofaune des recifs coralliens de Tulear (Madagascar): ecologie et relations trophiques. Annexe D.Sc. these, Univ. Aix-Marseille II, 116 p. [In French.]
1981. Trophic relationships of reef fishes in Tulear (Madagascar). Oceanol. Acta 4:365–374.

Hayes, T. A., T. F. Hourigan, S. C. Jazwinski Jr., S. R. Johnson, J. D. Parrish, and D. J. Walsh.
1982. The coastal resources, fisheries and fishery ecology of Puako, West Hawaii. Hawaii Cooperative Fishery Research Unit Tech. Rep. 82-1, 159 p.

Hiatt, R. W., and D. W. Strasburg.
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65–127.

Hobson, E. S.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. 70:715–740.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 72:915–1031.

Humason, G. L.
1979. Animal tissue techniques, 4th ed. Freeman, San Francisco, 661 p.

Johannes, R. E.
1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fishes 3:65–84.

Khoo, H. K.
1978. The histochemistry and endocrine control of vitellogenesis in goldfish ovaries. Can. J. Zool. 57:617–626.

Loubens, G.
1980. Biologie de quelques especes de Poissons du lagon neo-caledonien. II: Sexualite et reproduction. Cahiers de l'Indo-pacifique 2(1):41–72. [In French.]

Maragos, J. E., and P. L. Jokiel.
1986. Reef corals of Johnston Atoll: one of the world's most isolated reefs. Coral Reefs 4:141–150.

Munro, J. L.
1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Part V.m: Summary of biological and ecological data pertaining to Caribbean reef fishes. ODA/UWI Fisheries Ecology Research Project: 1969–1973. Research report from the Zoology Dept., Univ. West Indies. No. 3. Kingston, Jamaica, 24 p.

Munro, J. L., V. C. Gaut, R. Thompson, and P. H. Reeson.
1973. The spawning seasons of Caribbean reef fishes. J. Fish Biol. 5:69–84.

Norris, J. E., and J. D. Parrish.
1988. Predator-prey relationships among fishes in pristine coral reef communities. *In* J. H. Choat et al. (eds.), Proc. sixth int. coral reef symposium, Townsville, Australia, 8–12 Aug. 1988, vol. 2, p.107–113. Sixth Int. Coral Reef Symp. Exec. Comm.

Oda, D. K., and J. D. Parrish.
1982. Ecology of commercial snappers and groupers introduced to Hawaiian reefs. *In* E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh Jr., and R. T. Tsuda (eds.), Proc. fourth int. coral reef symposium, Manila, 18–22 May 1981, vol. 1, p. 59–67. Marine Sciences Center, Univ. Philippines, Quezon City, Philippines.

Parrish, J. D.
1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Mar. Ecol. Prog. Ser. 58:143–160.

Parrish, J. D., M. W. Callahan, and J. E. Norris.
1985. Fish trophic relationships that structure reef communities. *In* C. Gabrie and B. Salvat (eds.), Proc. fifth int. coral reef congress, Tahiti, 27 May–1 June 1985, vol. 4, p. 73–78. Antenne Museum-EPHE, Moorea, French Polynesia.

Pinkas, L., M. S. Oliphant, and I. Iverson.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152:1–105.

Porter, J. W., and K. G. Porter.
1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol. Oceanogr. 22: 553–556.

Randall, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665–847.

Randall, J. E., and P. Gueze.
1981. The holocentrid fishes of the genus *Myripristis* of the Red Sea, with clarification of the *murdjan* and *hexagonus* complexes. Los Angel. Cty. Mus. Contrib. Sci. 334, 16 p.

Randall, J. E., P. S. Lobel, and E. H. Chave.
1985. Annotated checklist of the fishes of Johnston Island. Pac. Sci. 39:24–80.

Sale, P. F.
1985. Patterns of recruitment in coral reef fishes. *In* C. Gabrie and B. Salvat (eds.), Proc. fifth int. coral reef congress, Tahiti, 27 May–1 June 1985, vol. 5, p. 391–396. Antenne Museum-EPHE, Moorea, French Polynesia.

Schroeder, R. E.
1985. Recruitment rate patterns of coral reef fishes at Midway lagoon, Northwestern Hawaiian Islands. *In* C. Gabrie and B. Salvat (eds.), Proc. fifth int. coral reef congress, Tahiti, 27 May–1 June 1985, vol. 5, p. 379–384. Antenne Museum-EPHE, Moorea, French Polynesia.

ter Kuile, C.
1989. The forage base of some reef fishes in the Flores Sea with notes on sampling and fishery. Neth. J. Sea Res. 23:171–179.

Victor, B. C.
1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. (Berl.) 71:203–208.

Vivien, M. L., and M. Peyrot-Clausade.
1974. A comparative study of the feeding behaviour of three coral reef fishes (Holocentridae), with special reference to the polychaetes of the reef cryptofauna as prey. *In* A. M. Cameron, B. M. Campbell, A. B. Cribb, R. Endean, J. S. Jell, O. A. Jones, P. Mather, and F. H. Talbot (eds.), Proc. second int. symp. coral reefs, Great Barrier Reef Province, Australia, 22 June–2 July 1973, vol. 1, p. 179–192. The Great Barrier Reef Committee, Brisbane.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Walsh, W. J.
1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Environ. Biol. Fishes 18:257–276.

Watson, W., and J. M. Leis.
1974. Ichthyoplankton in Kaneohe Bay, Hawaii. A one year study of fish eggs and larvae. Univ. Hawaii Sea Grant Technical Report TR–75–01, 178 p.

Williams, D. M.
1983. Daily, monthly and yearly variation in recruitment of juvenile coral reef fishes to coral habitats within One Tree Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 65:245–253.

Winn, H. E., J. A. Marshall, and B. Hazlett.
1964. Behavior, diel activities, and stimuli that elicit sound production and reactions to sounds in the longspine squirrelfish. Copeia 1964:413–425.

Wolfert, D. R., and T. J. Miller.
1978. Age, growth, and food of northern pike in eastern Lake Ontario. Trans. Am. Fish. Soc. 107:696–702.

Wyatt, J. R.
1976. The biology, ecology, exploitation and management of Caribbean reef fishes. Va: The biology, ecology and bionomics of Caribbean reef fishes: Holocentridae (squirrelfishes). ODA/UWI Fisheries Ecology Research Project: 1969–1973. Research report from the Zoology Dep., Univ. West Indies. No. 3. Kingston, Jamaica. 41 p.

Wyrtki, K.
1974. Sea level and seasonal fluctuations of the equatorial currents in the western Pacific Ocean. J. Physical Oceanogr. 4:91–103.

Appendix A

Relationships between standard length (SL), fork length (FL), and total length (TL) in millimeters, based on linear regressions for 377 specimens of the brick soldierfish, *Myripristis amaena,* from Johnston Atoll (JA).

$$SL = 0.9013\ FL - 3.22, \quad r^2 = 0.991$$
$$SL = 0.7811\ TL - 3.23, \quad r^2 = 0.992$$
$$TL = 1.1493\ FL + 0.65, \quad r^2 = 0.991$$

Appendix B

Size measured and batch fecundity estimated by counting ova in aliquots from the ovaries of 12 specimens of the brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA).

Standard body length (mm)	Whole body wet weight (g)	Estimated batch fecundity
156	149	12402
166	162	12925
168	167	17077
169	166	17618
175	189	29505
175	187	57200
177	191	47680
179	190	42003
180	189	25301
181	225	69221
187	209	61000
188	211	66719

Reproductive biology of the cockfish, *Callorhynchus callorhynchus* (Holocephali: Callorhynchidae), in Patagonian waters (Argentina)

Edgardo E. Di Giácomo
Maria Raquel Perier
Instituto de Biología Marina y Pesquera "Alte. Storni"
CC 104, 8520 San Antonio Oeste, Río Negro, Argentina

Abstract.—*Callorhynchus callorhynchus* Linnaeus ("cockfish" or "pez gallo"), the only holocephalan fish species found in the coastal waters of the southwestern Atlantic Ocean, has been caught off Argentina as bycatch of the hake, *Merluccius hubbsi*, fishery since 1920. Here we describe the morphology of its reproductive system and report on several aspects of its reproductive biology. This study is based on survey data and sampling of commercial landings from San Matías Gulf (41–42°S; 64–65°W), conducted from 1984 to 1986.

The data suggest that reproductive activities extend nearly throughout the year; mating and spawning occur in spring and early summer, followed by a short period (ca. one month) of gonadal recovery. Average size at sexual maturity (standard length, measured from the tip of the mouth to the origin of the superior caudal lobe) is 40 cm for males and 49 cm for females. Male gonadal and green gland indices peak asynchronously. During the mating season the green gland forms spermatophores that are transferred to the female at the time of copulation. The cloaca of adult females has a seminal receptacle where the mass of spermatophores is stored after copulation. Female gonadal and nidamental gland indices peak synchronously. After fertilization the oocytes are encapsulated before spawning. Oocyte diameter increases with the size of females up to a maximum of 48 mm.

Manuscript accepted 26 January 1994.
Fishery Bulletin 92: 531–539 (1994).

The cockfish, *Callorhynchus callorhynchus* Linnaeus, 1758, is the only holocephalan fish species found in the coastal waters of the southwestern Atlantic Ocean (Norman, 1937; Hart, 1946; Menni and Gostonyi, 1982). Adults are caught as bycatch of the hake, *Merluccius hubbsi*, fishery that operates off Argentina (Di Giácomo and Perier, 1991). Although there is considerable concern with regard to harvesting fish species with comparatively low reproductive potential (such as many elasmobranch and holocephalan species), the reproductive biology and life history of the cockfish are poorly known. In this study we describe the morphology of the reproductive system of *C. callorhynchus* and present information on its reproductive biology.

Materials and methods

Bottom trawl surveys

A survey off the north coast of San Matías Gulf (northern Patagonia; 41–42°S, 64–65°W; Fig. 1) was conducted from 15 to 19 October, 1986, aboard the FRV *C. Cánepa*. Thirty three 30-minute hauls were made at depths ranging from 20 m to 130 m, by using a 96-foot commercial otter trawl with rectangular doors (Di Giácomo and Perier, 1991). All specimens of *C. callorhynchus* were processed following laboratory procedures described below.

Sampling of the commercial landings

The commercial catch of the bottom trawl fishery landed in San Antonio Oeste (40°43'04"S, 64°56'W) was sampled monthly between February 1984 and July 1986. On each sampling date three boxes (N=20 fish per box) weighing 37 kg each were randomly selected. Samples of the commercial catch were not available during April, September, June, and December because either the fishery was inactive or no cockfish were landed.

Laboratory procedures

Standard length (SL, distance from the tip of the snout to the origin of the upper caudal lobe, Fig. 2A), total weight and liver weight were obtained from each fish sampled. Specimens were dissected to expose the reproductive system; testes and green glands of males, and ovaries and nidamental glands of females were individually weighed. The number of mature yolk oocytes and immature oocytes, maximum diam-

eter of the oocytes, number of individuals with egg cases in formation or ready for extrusion, and presence of spermatophores were recorded for females. Length of the myxopterygia (males) was measured from the insertion of the pelvic fin to the distal end (Fig. 2B).

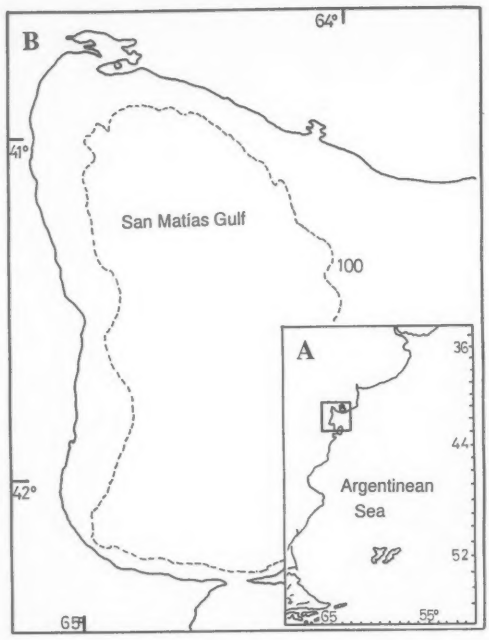


Figure 1

(**A**) Location of the study area in the Argentinean continental shelf; (**B**) San Matías Gulf.

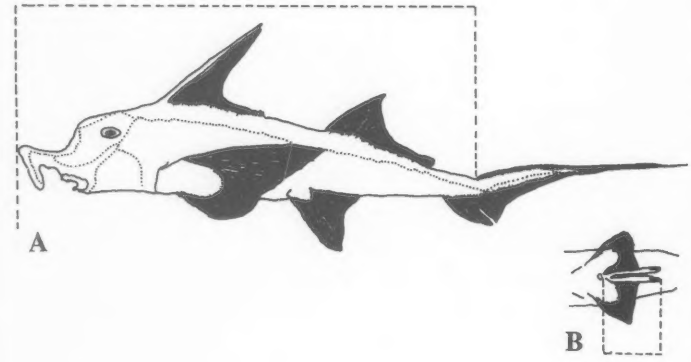


Figure 2

Measurements for cockfish, *Callorhynchus callorhynchus*. (**A**) Standard length; (**B**) myxopterygia length in male.

Indices of reproductive activity

The annual reproductive cycle was assessed by using the monthly samples of the commercial catch (1984–86). The gonadal index (GI), hepatic index (HI), nidamental gland index (NGI, females only) and green gland index (GGI, males only) were calculated as

$$GI = \frac{\text{weight of the gonad}}{\text{total weight}} \times 100$$

$$HI = \frac{\text{weight of the liver}}{\text{total weight}} \times 100$$

$$NGI = \frac{\text{weight of the nidamental gland}}{\text{total weight}} \times 100$$

$$GGI = \frac{\text{weight of the green gland}}{\text{total weight}} \times 100.$$

The duration of the mating season was estimated from the presence of spermatophore masses in the female cloaca and the annual cycle of the green gland index.

Regression analysis was performed between the indices of reproductive activity during the periods of maximum activity and SL, and between the diameter of mature oocytes and the number of immature oocytes and SL. A Wilcoxon test was used to assess the difference in the average number of mature ova between right and left ovaries of all mature females.

Sexual maturity

The degree of development of the myxopterygia (male claspers) relative to SL was used as an indicator of sexual maturity for males (Holden and Raitt, 1975). The size at first maturity in females was determined by examining 1) the percentage of mature females in each 10-mm size class, 2) the maximum diameter of mature ovarian eggs for each size class, and 3) the smallest size class with egg cases in formation. Females with yellow ovarian eggs were considered mature.

Results

Morphology of the reproductive system

The male reproductive system consists of the following paired struc-

tures: testes, epididymis (efferent ducts), and deferent ducts (Leigh-Sharpe, 1922). In sexually mature individuals, the deferent ducts are differentiated into two fusiform structures called green glands (Fig. 3A). These structures agglutinate the spermatozoa into spermatophores and secrete a gelatinous, green fluid. The reproductive system of the female is composed of the following paired structures: ovaries, oviducts, nidamental or shell glands, uteri, and vaginal openings that end in a cloaca (Fig. 3B).

Holocephalans are sexually dimorphic. Male secondary sexual structures (frontal tenaculum, and prepelvic and pelvic claspers) are utilized during mating (Fig. 4); the male apparently inserts the mass of spermatophores into the seminal receptacle of the female cloaca. Upon macroscopic examination (October), a mass of spermatophores was found at the female genital opening. Spermatozoa are liberated progressively by an unknown mechanism, before fertilization.

Females extrude fertilized eggs enclosed within a leathery case (Dean, 1906) that acts as protection for the embryo during development. At hatching the fry resembles the adult.

Indices of reproductive activity

The GI of males reached a maximum in March (3.0) and was low from July to October (range seen in Fig. 5A). The highest mean values of the GGI were found between July and October (Fig. 5B), although the index was also high during January and February. In females, the GI reached its highest values from July to October, indicating low reproductive activity during the rest of the year (Fig. 6A). The NGI (females) has two periods of activity: July to November (highest) and January to June (lowest) (Fig. 6B). The HI for both males and females (Fig. 5C, 6C) did not show significant annual fluctuations; maximum values occurred simultaneously with peaks in the other reproductive indices.

Mature and immature females could be differentiated based on GI values (range: 0.13 to 4.55); a GI value larger than 1.0 was characteristic of mature females. The presence in March of some females smaller than 50 cm SL with a GI higher than 1.0 and ovaries with translucent oocytes was suggestive of oocyte resorption. Oocyte diameter varied between 10 and 35 mm.

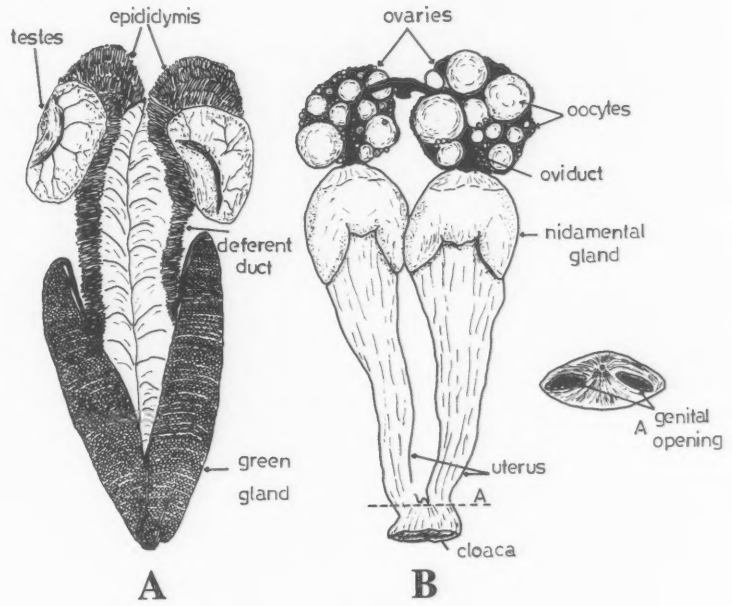


Figure 3

Reproductive organs of the cockfish, *Callorhynchus callorhynchus*. (**A**) Males; (**B**) females.

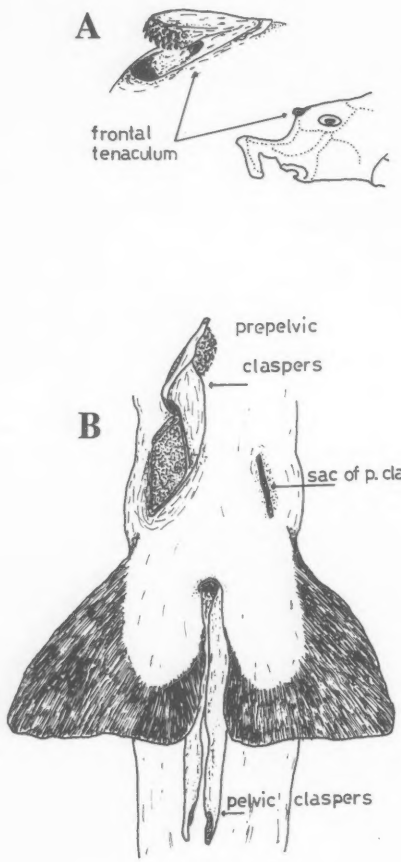


Figure 4

Male secondary sexual structures of cockfish, *Callorhynchus callorhynchus*. (**A**) Frontal tenaculum; (**B**) prepelvic and pelvic claspers.

Gonad and green gland indices were highly variable within size classes during the period of maximum activity. There was no relationship between SL and GI (r^2=0.001; P>0.05; N=121), or between SL and GGI (r^2=0.021; P>0.05; N=101). Similarly, no relationship was found between female SL and GI (r^2=0.18; P>0.05; N=58) or NGI (r^2=0.012; P>0.05; N=48).

Size at sexual maturity

Immature and mature males could be identified from the relationship between SL and length of the myxopterygia. The myxopterygia did not exceed the posterior margin of the pelvic fin in immature individuals, whereas in mature individuals it consisted of partially calcified structures that exceeded the posterior margin of the pelvic fin. The length of fish measured (N=123) ranged from 26 cm to 55 cm. Length at first maturity of males was estimated to be 40 cm, corresponding to a length of the myxopterygia of 45 mm. No individuals between juvenile and mature stages were observed. Juvenile stages were found in shallow waters (depth range 15–25 m) whereas adults were found in waters deeper than 25 m (Di Giácomo, 1992). Most mature females were larger than 50 cm (SL), whereas all females smaller than 48 cm were immature.

Ovarian maturation

The percentage of mature oocytes was greatest in August in both ovaries, coinciding with maxima in the indices of reproductive activity. Nevertheless, some mature oocytes were observed throughout the year (Fig. 7A). Mean number of mature oocytes was highest from July to October. There was a significant difference between the average number of mature oocytes in the right and left ovaries of individual mature females (Wilcoxon test, P<0.05; Fig. 7B).

Oocyte diameter increased with female size (r^2=0.083; P<0.01; N=90). Maximum oocyte diameter (48 mm) was recorded for a female of 71 cm SL. The regression of number of immature oocytes on SL showed a similar trend, indicating that average reproductive potential increases with size (r^2=0.024; P<0.01; N=101).

Oocytes smaller than 10 mm (diameter) were translucent to lightly whitish. Coloration of oocytes larger than 10 mm changed gradually. Yolk was incorporated until the oocytes reached complete development and passed to the nidamental gland. Production of egg cases began in the nidamental gland, when the oocytes reached maturity. The closed end of the egg case was caudally oriented; the cephalic portion remained open until the case was completely formed. When the egg case was about two-thirds of its final size, ovulation occurred and the egg (with a variable diameter that ranged from 40 to 48 mm) moved from the ovaries, through the oviduct, to the case.

Mating season

Spermatophores were found in the vaginal receptacles associated with the female cloaca. Mating occurred primarily from July to February, when maxima in the GGI were indicative of active production of spermatophores. The highest percentage of females with spermatophores in the cloaca was also observed during these months (Fig. 8). In October, recently deposited spermatophores in the female cloaca, characterized macroscopically by an intense green color, resembled green gland products. Yellowish spermatophores found in March and May (when

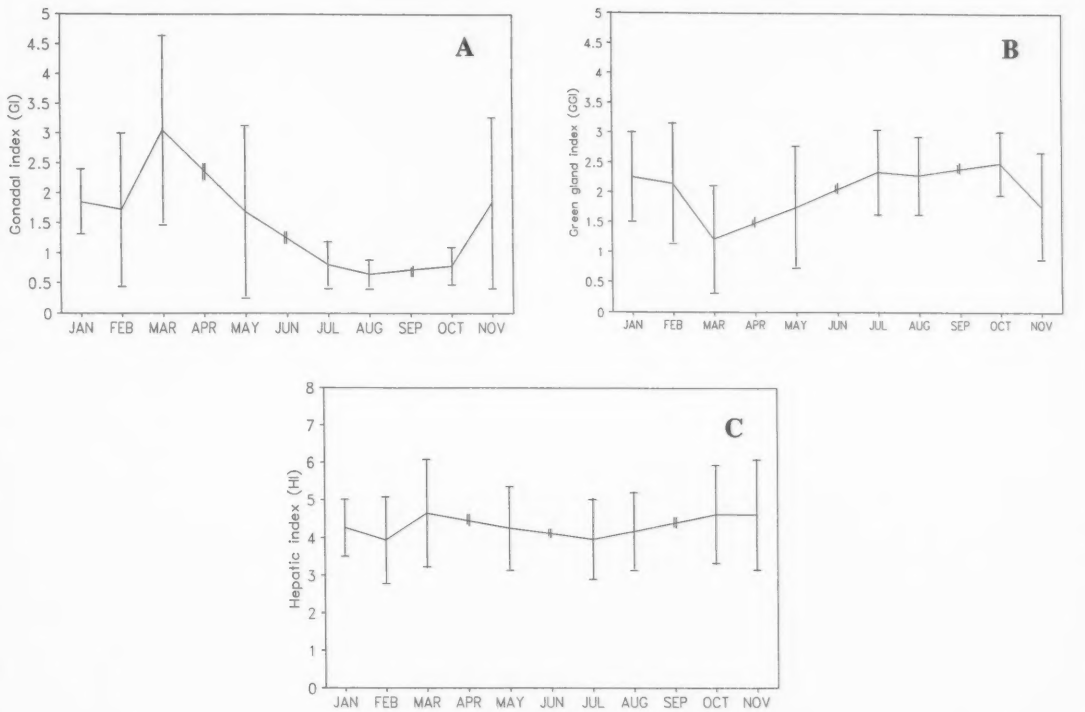


Figure 5

Indices of reproductive activity of males of the cockfish, *Callorhynchus callorhynchus*. (**A**) Gonadal index (GI); (**B**) green gland index (GGI); (**C**) hepatic index (HI).

the green gland index was low) probably remained from copulation during the previous year. After insemination, the spermatophores were apparently mobilized by the female in coordination with the production of egg cases in order to fertilize the oocytes.

Spawning season

The primary spawning season extended from July to November. The mean size of females with egg cases in formation increased from July to November (Fig. 8). Egg cases in an early stage of development were found in bottom trawl catches at 105 m, whereas females with egg cases with embryos almost fully developed were found in bottom dredge catches at depths ranging from 20 to 40 m.

Discussion

Morphology

The morphology of the reproductive system of holocephalan fishes has been described for *Chimaera monstrosa* and *Callorhynchus antarcticus* (Leigh-Sharpe, 1922; Legendre, 1944), and *Hydrolagus colliei* (Cox, 1963). Species of living holocephalans are generally reported to lack a cloaca (Grasse, 1958; Lagler et al., 1977); Malagrino et al. (1981) mentioned the absence of a cloaca in females of *Chimaera phantasma* as characteristic of the group. This contrasts with the elasmobranchs, in which the female genital ducts terminate in the cloaca. Stanley (1963) noted the presence of a cloaca in newly hatched males and females of *H. colliei*, which is lost as they grow. *Callorhynchus callorhynchus*, by contrast, has a cloaca with a seminal receptacle where the spermatophores are stored.

Reproductive cycle

The peak of the male GI indicates the season when testicular activity is at a maximum. The delay between maxima in GGI and GI may reflect a sequence of phenomena: 1) production of spermatozoa in the testes, 2) movement of spermatozoa through the ef-

ferent ducts and the first part of the deferent ducts, and 3) accumulation in the green gland during the formation of spermatophores. Activity of the female gonads and nidamental glands is synchronous because as the oocytes mature they are ovulated and immediately encapsulated in the nidamental glands.

Unlike most elasmobranch species in which one ovary is functional and the other is vestigial (Mellinger, 1972; Menni et al., 1979; Teshima, 1981; Natanson and Cailliet, 1986; Smith and Merriner, 1986), the left and right ovaries of *C. callorhynchus* are both functional. However, the average number of ova produced in each ovary is different. As in *H. colliei*, the egg cases of *C. callorhynchus* are produced simultaneously by both of the nidamental glands (Dean, 1906).

Changes taking place in the development of the gonad and the green gland of males suggest that reproductive activity is continuous, with a period of rest or recovery around March. Relatively high female index values in February can be considered a continuation of the main period of reproductive activity. The sample of females analyzed in January was probably not representative because of their scarcity in commercial landings. Resting or recovery may last one or two months in *C. callorhynchus*, while males and females of *C. monstrosa* and *C. phantasma* have a resting period of six months (Vu Tan Tue, 1972; Malagrino et al., 1981).

Sexual maturity

A threshold value in the GI has been utilized to separate immature and mature females in some teleost species in which oocytic resorption has not been observed. In *C. callorhynchus* such a GI threshold criterion must be coupled with macroscopic observation of the ova in the ovary; in the case of low GI values, presence or absence of atrophied ova is indicative of resting or immature conditions, respectively.

Development of the myxopterygia is diagnostic of male maturity in *C. callorhynchus*, allowing the identification of the length at first maturity. Transition between stages can be related to an offshore migra-

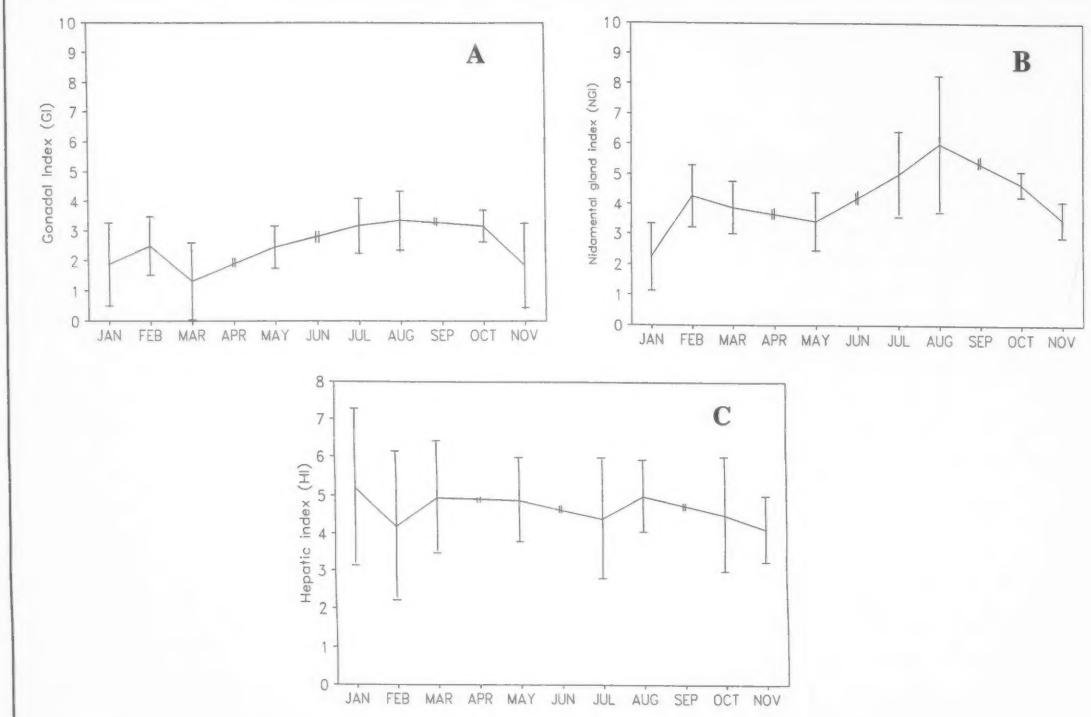


Figure 6

Indices of reproductive activity of females of the cockfish, *Callorhynchus callorhynchus*. (**A**) Gonadal index (GI); (**B**) nidamental gland index (NGI); (**C**) hepatic index (HI).

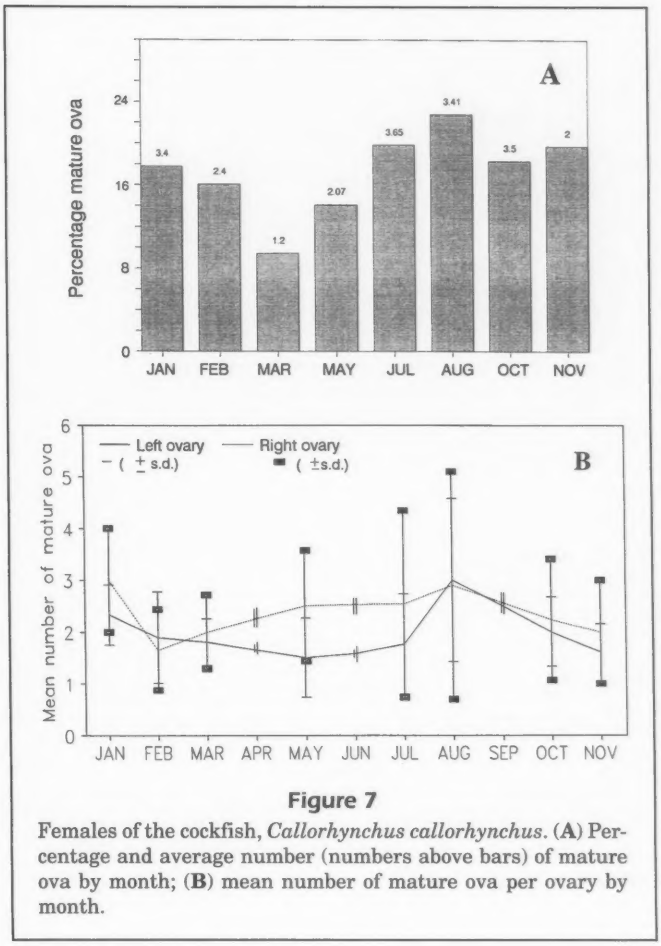


Figure 7

Females of the cockfish, *Callorhynchus callorhynchus*. (**A**) Percentage and average number (numbers above bars) of mature ova by month; (**B**) mean number of mature ova per ovary by month.

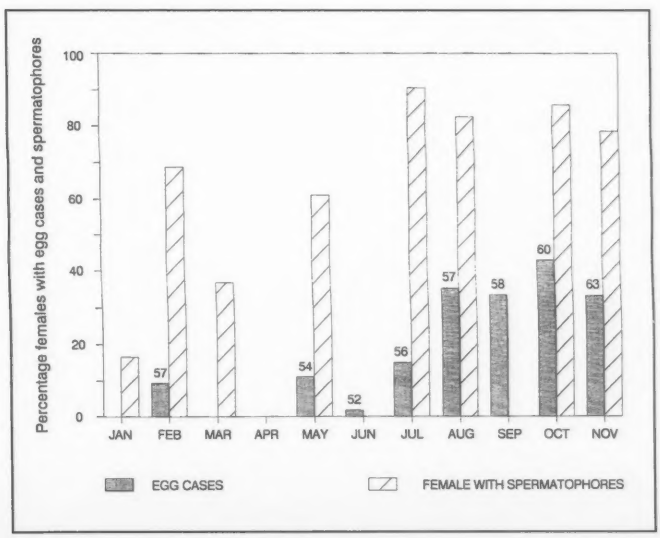


Figure 8

Percentage of spermatophores and developing egg cases in females of the cockfish, *Callorhynchus callorhynchus*, by month.

tion. The absence of intermediate stages in our materials can be explained by the fact that sampling was conducted mostly between 90 and 130 meters, where adults prevail (Di Giácomo, 1992).

Mature females cannot be clearly defined. Holden (1975) defined mature females of the ray *Raja clavata* as those individuals that had large, yellow oocytes in the ovaries. Smith and Merriner (1986) distinguished three stages of sexual maturity in females of the cownose ray, *Rhinoptera bonasus*: immature, maturing, and mature. The mature stage was characterized by the presence of large, yellow oocytes greater than one cm in diameter in the ovaries. The authors accounted for the minimum length of gravid females observed (*R. bonasus* is viviparous). We could not identify which oocytes were ready to be spawned in *C. callorhynchus*. Although all yellow oocytes were viable, resorption may lead to false conclusions regarding spawning state. Therefore, the minimum size fish that had egg cases in formation in the nidamental gland was considered diagnostic, since at that stage resorption is no longer possible. The smallest female with egg cases in formation measured 50 cm (SL), and the smallest female with mature oocytes was 48 cm SL. In females size at first maturity was coincident with the minimum size of fish showing yolked oocytes and egg cases in formation.

McEachran (1970) found that in females of the ray *Raja garmani* the oocytes in the ovaries were half the size of those found in the egg cases. In *C. callorhynchus*, the difference between the maximum size attained by the oocytes in the ovaries and the eggs in the case was about 25%. Assuming a similar speed of yolk incorporation into the oocytes for both species, we estimate that the females of *C. callorhynchus* may have a higher spawning rate than the ray, indicating that maturing oocytes may attain ovulation size faster. The maximum size of mature ova was larger in *C. callorhynchus* than in other holocephalan species such as *Chimaera phantasma* (Malagrino et al., 1981), *C. monstrosa*

(Legendre, 1944), *Hydrolagus colliei* (Dean, 1906), and *Callorhynchus milii* (Gorman, 1963).

Spermatophores

The presence of a "seminal plug" has been reported in *C. milii* (Norman, 1937). Males of *C. monstrosa* form an emerald green substance in the terminal portion of the deferent ducts, but seminal plugs in females have not been reported (Legendre, 1944). There is no seminal plug in *H. colliei*, in which copulation occurs just before eggs are laid (Dean, 1906).

On the basis of our examination of *C. callorhynchus*, we suggest that the term "plug" is improper. It is a seminal mass located in the female's seminal receptacle that does not obstruct the genital ducts and remains in the receptacle during the entire reproductive cycle. The coloration of the spermatophores in the cloaca changes progressively from an intense green to yellow as the spermatophores are mobilized.

Spawning ground

Although we demonstrated seasonality in the mating activity of *C. callorhynchus*, it was not possible to establish where spawning takes place. Quinn et al. (1980) suggested that adults of *H. colliei* migrate to shallow waters during the night. Eighty-five egg cases of *H. colliei* were found at a depth of 11 m, but one capsule was found at 120 m (Dean, 1906). *Callorhynchus monstrosa* spawns at about 100 m (Legendre, 1944); based on its bathymetric distribution (100 to 1700 m), it can be assumed that this species also migrates to the relatively shallow areas to spawn. Females of *C. milii* lay eggs between the surf zone and 37 m, in sand or mud substrata, and move to deeper water after spawning (Gorman, 1963).

Callorhynchus callorhynchus was caught at depths shallower than 170 m in the San Matías Gulf (Di Giácomo, 1992). Egg cases were found between 20–40 m and at 104 m, suggesting that this species may also migrate to shallow water to spawn. Further studies are required to document more conclusively the spawning behavior of females.

Acknowledgments

We wish to thank Miriam Fernandez, Oscar Iribarne, and Ted Pietsch (University of Washington, Seattle) for criticism of an earlier version of the manuscript; comments from R. Hardy, two anonymous referees, and Lobo Orensanz and Ana Parma were helpful in shaping the final version. This research was supported by the Ministry of Economics (Rio Negro Province), the National University of the Comahue, and the National Secretary of Science and Technology (Argentine).

Literature cited

Cox, K. W.
1963. Egg-cases of some elasmobranchs and a cyclostome from Californian waters. Calif. Fish Game 49:271–289.

Dean, B.
1906. Chimaeroid fishes and their development. Publ. Carnegie Inst., Washington, 32, 195 p.

Di Giácomo, E. E.
1992. Distribución de la población del pez gallo (*Callorhynchus callorhynchus*) en el golfo San Matías, Argentina. Frente Maritimo 12(A):113–118.

Di Giácomo, E. E., and M. R. Perier.
1991. Evaluación de la biomasa y explotación comercial del pez gallo (*Callorhynchus callorhynchus*) en el Golfo San Matías, Argentina. Frente Maritimo 9(A):7–13.

Gorman, T. B. S.
1963. Biological and economic aspects of the elephant fish, *Callorhynchus milii* Bory, in Pegasus Bay and the Canterbury Bight. New Zealand Marine Dep. Fisheries Tech Rep. 8, 53 p.

Grasse, P. P.
1958. Super-ordre des holocephali: anatomie, ichtyologie, systematique. *In* Pierre-P. Grasse (ed.), Traite de zoologie; anatomie, systematique, biologie, Vol. 13, Agnathes et poissons, p. 2060–2067. Masson et Cie, Paris.

Hart, J.
1946. Report on trawling surveys on the Patagonian Shelf. Discovery Rep. 23.

Holden, M. J.
1975. The fecundity of *Raja clavata* in British waters. J. Cons. int. Explor. Mer 36:110–118.

Holden, M. J., and D. F. S. Raitt (eds.).
1975. Manual de Ciencia pesquera. Parte 2: Métodos para investigar los recursos y su aplicación. Doc. Téc. FAO Pesca 115 (Rev. 1), 211 p.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. May Passino.
1977. Ichthyology (2nd. ed.). John Wiley & Sons, 506 p.

Legendre, R.
1944. Notes biologiques sur *Chimaera monstrosa* L. Bull. Soc. Zool. France 69:10–17.

Leigh-Sharpe, W. H.
1922. The comparative morphology of the secondary sexual characters of Holocephali and elasmobranch fishes. J. Morphol. 36: 199–243.

Malagrino, G., A. Takemura, and K. Mizue.
1981. Studies on Holocephali. II: On the reproduction of *Chimaera phantasma* Jordan et Snyder caught in the coastal waters of Nagasaki. Bull. Fac. Nagasaki Univ. 51:1–7.

McEachran, C. P.
1970. Egg capsules and reproductive biology of the skate *Raja garmani* (Pisces: Rajidae). Copeia 1970:197–198.

Mellinger, J.
1972. Croissance et reproduction de la torpille (*Torpedo marmorata*). I: Introduction, ecologie, croissance generale et dimorphisme sexuel. Cycle. Fecondite. Bull. St. Biol. Arcachon 24:166–218.

Menni, R. C., and A. E. Gostonyi.
1982. Benthic and semidemersal fish associations in the Argentine Sea. Stud. Neotrop. Fauna Environ. 17:1–29.

Menni, R. C., A. E. Gostonyi, and H. L. López.
1979. Sobre la ecología y biología de *Halaelurus bivius* (Chondrichthyes, Scyliorhinidae). Rev. Museo Arg. Cienc. Nat. (Ecología) 2(3):71–88.

Natanson, L. J., and G. M. Cailliet.
1986. Reproduction and development of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. Copeia 1986:987–994.

Norman, J. R.
1937. Coast fishes. Part II: The Patagonian region. Discovery Rep. 16:35–36.

Quinn, T. P., B. S. Miller, and R. C. Wingert.
1980. Depth distribution and seasonal and diel movements of ratfish, *Hydrolagus colliei*, in Puget Sound, Washington. Fish. Bull. 78:816–821.

Smith, J. W., and J. V. Merriner.
1986. Observations on the reproductive biology of the cownose ray, *Rhynoptera bonasus*, in Chesapeake Bay. Fish. Bull. 84:871–877.

Stanley, H. P.
1963. Urogenital morphology in the chimaeroid fish *Hydrolagus colliei* (Lay and Bennett). J. Morphol. 112:99–128.

Teshima, K.
1981. Studies on the reproduction of Japanese smooth dogfishes *Mustelus manazo* and *M. grisseus*. Bull. Shimonoseki Univ. Fish. 29:115–199.

Vu Tan Tue.
1972. Variations cycliques des gonades et de quelques glandes endocrines chez *Chimaera monstrosa* Linné (Pisces: Holocephali). Ann. Sci. Nat. (Zool.) 12(14):49–94.

The vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska*

Arthur W. Kendall Jr.
Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115

Lewis S. Incze
Bigelow Laboratory for Ocean Sciences
West Boothbay Harbor, Maine 04575

Peter B. Ortner
Shailer R. Cummings
Atlantic Oceanographic and Meteorological Laboratory
4301 Rickenbacker Causeway, Miami, Florida 33149

Patricia K. Brown
Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115

Abstract.—The vertical distribution of walleye pollock eggs and larvae in Shelikof Strait, Gulf of Alaska, was investigated by using data from 36 Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) tows taken in April and May, 1986–88. Most eggs were found below 150 m to near bottom (~300 m) but progressively shallower later in the season. Eggs in middle stages of development were found at shallower depths than were younger or older eggs. The vertical distribution of eggs was positively related to observed differences in seawater temperature but showed no relationship to density. Larvae hatch at incubation depth and quickly rise to the upper 50 m of the water column where they remain during larval development. Larger larvae (~7–10 mm standard length [SL]) undergo limited diel vertical migration within the upper 50 m. They are deepest during the day, shallowest at dusk, slightly deeper at night, and even deeper at dawn. Their mean depths of occurrence were between 21 and 37 m at all times. At these depths, prey (copepod nauplii) generally were at densities sufficient for larval pollock growth as determined in laboratory studies. Pronounced thermoclines and pycnoclines were present in the part of the water column inhabited by the larvae in late May. Larvae appear to remain below the upper mixed layer during periods of increased turbulence, but at depths during daytime where light was sufficient for feeding and where prey densities were adequate.

The vertical distributions and movements of planktonic organisms must be studied to understand their population dynamics. Often individual populations undergo vertical migrations and inhabit different advective and thermal regimes on a daily cycle (e.g. Hardy, 1936; Enright, 1977). The entire planktonic community may migrate similarly, or different organisms may cooccur on a diel cycle. The reasons for diel vertical migrations of ichthyoplankton may be related to feeding-digestion cycles, enhanced predator avoidance, or directed transport (Norcross and Shaw, 1984; Lampert, 1989).

Planktonic eggs of most marine fishes occur in the upper water column, although there are exceptions (Ahlstrom, 1959; Coombs et al., 1981). Neilson and Perry (1990) reviewed literature on vertical migration in fishes, particularly larvae of marine fishes, and attempted to identify common patterns and underlying causal mechanisms. They concluded that changes in depth distribution of larvae, while possibly under endogenous control, seem to be mediated by a number of environmental factors. While light and gravity dominate, other factors such as hydrography, food, tidal currents, and turbulence may also be important (Neilson and Perry, 1990; Lough and Potter, 1993). Planktonic larvae of fishes are found generally at shallower depths at night than during the day (Kendall and Naplin, 1981) although the opposite pattern also occurs (Boehlert et al., 1985; Yamashita et al., 1985; Sogard et al., 1987). In some species inconsistent patterns have been found among studies, possibly indicating the confounding effects of several biotic and

Manuscript accepted 31 January 1994.
Fishery Bulletin 92:540–554 (1994).

* Contribution 0177 of the Fisheries-Oceanography Coordinated Investigations.

abiotic factors (Sclafani et al., 1993). Vertical migrations in ichthyoplankton usually take place within the upper water column and may be correlated with the vertical distribution of larval fish prey (Munk et al., 1989; Pritchett and Haldorson, 1989). In some species the vertical extent of diel migrations increases as larvae grow (Ellertson et al., 1981; Yamashita et al., 1985).

In early April a large population of walleye pollock, *Theragra chalcogramma*, spawns in a restricted region of Shelikof Strait, Gulf of Alaska. The resulting planktonic eggs and larvae can be found, often in large patches, through April and May. Recruitment variation of this population has been examined, particularly those factors affecting interannual fluctuations in egg and larval mortality (Schumacher and Kendall, 1991).

Previous studies of the vertical distribution of walleye pollock eggs and larvae in Shelikof Strait have relied upon unmonitored discrete depth sampling (Kendall et al., 1987; Kendall and Kim, 1989). They have suggested that eggs occur generally below 150 m, and systematically change depth during their ~14-day incubation. Most larvae in these studies were found in the upper water column between about 10 and 50 m, but they migrated vertically. They seemed to congregate near the upper part of this range around sunrise and sunset, were situated somewhat deeper during midday, and were distributed more uniformly at night. A similar pattern for larval walleye pollock has been observed in other parts of the North Pacific (Kamba, 1977; Pritchett and Haldorson, 1989; Walline[1]).

The present study describes the vertical distribution of walleye pollock eggs and larvae in relation to changing environmental factors, measured on several dates in Shelikof Strait. This study is based on the analysis of 36 MOCNESS tows (Multiple Opening-Closing Net and Environmental Sensing System; Weibe et al., 1976) made over a period of three years. We examine ontogenetic changes in vertical distribution of eggs and larvae, and relate observed patterns to estimated ambient light and to measured temperature, salinity, and seawater density. Effects of vertical distribution of larval prey and changes in mixed layer depth due to wind events are also considered.

Materials and methods

MOCNESS tows were made from the NOAA ship *Miller Freeman* during spring 1986, 1987, and 1988, in areas where high abundance of eggs or larvae were expected (Kendall and Picquelle, 1990) and had been detected by exploratory sampling. Details of sampling during these cruises are contained in Incze et al. (1987), Proctor (1989), and Lawrence et al. (1991). Some of the tows reported here (8–11 May 1986, series four) were also used in a study of the response of zooplankton to the passage of a storm (Incze et al., 1990). On each MOCNESS tow, seven or eight nets were deployed. The nets were towed obliquely at 0.8–1.0 m/second through selected depth intervals and opened and closed in sequence. Net depth, flowmeter readings, temperature, and salinity (1987 and 1988) were displayed in real-time and digitally recorded. The nets had a nominal mouth area of 1 m^2. Volumes filtered per tow ranged from 34 to 980 m^3 (mean=167 m^3). Net mesh was 0.153, 0.333, or 0.505 mm, depending on the size range of the larvae expected as well as other sampling objectives.

Depth intervals were based on previous studies indicating that the eggs occurred primarily below 150 m and the larvae primarily in the upper 50 m (Kendall et al., 1987; Kendall and Kim, 1989). Early in the season when eggs were predominant, we focussed on the lower water column (>150 m), which was subdivided into 20-m sampling strata. Later in the season, we subdivided the upper water column (<90 m) into 15-m sampling strata.

Samples were fixed in 4–5% formalin and shipped to the Polish Plankton Sorting Center in Szczecin, Poland, where fish eggs and larvae were separated, and walleye pollock eggs and larvae were identified and counted. Stage of development of eggs was determined in each tow taken early in the season according to Blood et al. (1994). When more than 100 eggs were present in a sample, a subsample of 100 was staged. The egg stage data then were compressed into six stage groups as in Kendall and Kim (1989). Standard length (SL) (to 0.1 mm) of the larvae in each sample was measured. A subsample of 50 larvae was measured when more than 50 larvae were present in a sample. Catches of eggs and larvae per depth interval are reported as numbers per 1,000 m^3 of water based on volume filtered as determined from digital flowmeter records and net-frame angle. Mean and standard deviations (SD) of numbers per 1,000 m^3 for each tow were computed from the weighted average of the numbers per 1,000 m^3 from each net within the tow, by using the length of the depth interval for each net as the weight. Estimation of egg and larval mean depth, larval mean length, and their standard deviations is based on cluster sampling where each tow represents a cluster, each net subsamples eggs and larvae from the cluster, and each egg or larva is an element within the cluster (Equations 8.1 and 8.2 in Scheaffer et al., 1986). The observation associated

[1] Walline, P D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June–July 1979. NWAFC Processed Rep. 81-05. Northwest and Alaska Fish. Cent., NMFS, NOAA, Seattle, WA 98115-0070, 22 p.

with each egg or larva, used to estimate mean depth, is the depth of the net where it was collected. Additionally, observations of lengths of larvae in each net were used to estimate mean lengths. Gaussian statistics, including analysis of variance (ANOVA) and analysis of covariance (ANCOVA), were used to compare mean depths of eggs and larvae and stages of eggs, and lengths of larvae with various environmental variables: time of day, temperature, salinity, and depth.

Temperature and salinity data from vertical Seabird conductivity, temperature, and depth (CTD) casts made in conjunction with the MOCNESS tows in 1986 were processed at the Pacific Marine Environmental Laboratory, Seattle. CTD data were collected with Seabird sensors on the MOCNESS in 1987 and 1988 and were processed at the Atlantic Oceanographic and Meteorological Laboratory, Miami. CTD data were available at 1-m depth intervals. In comparing temperature and density (expressed as σ_t) with depths of occurrence of eggs and larvae among tows, the mean and standard deviation of temperature and density were calculated within the depth interval of +/– one standard deviation of the mean depth of eggs or larvae. Egg mean depth weighted by abundance was regressed on temperature. Meteorological data from the Kodiak airport for the sampling periods in April and May 1986, 1987, and 1988 were used to model hourly irradiance at depth in the area by using an attenuation coefficient of 0.16 (a mean value of 33 measurements [SD=0.103] made aboard ship in Shelikof Strait between 3 and 23 May 1991[2]).

[2] Davis, R. AFSC. Personal commun., April 1992.

Data from the 36 tows were grouped into nine "series" that were numbered sequentially based on calendar day without regard to year. The first time series included eggs sampled on 12–16 April, and the ninth series included larvae sampled on 23–25 May. Tows within a series were taken with the same rationale; i.e. in a fixed location or following a drogue, with similar depth schemes, and close to the same dates (Table 1). Each series was composed of one to eight tows taken in areas of high egg and/or larval concentrations except series six and seven, which were taken primarily for zooplankton studies (Fig. 1). Series eight, in mid-May, was taken about seven weeks after peak spawning, in the spawning area. Series four and nine had time series sufficient to investigate diel differences in vertical distribution. Tows during these two series were taken at local midnight (midway between sunset and sunrise), dawn (sun 20° above the horizon), local noon, and dusk (sun 20° above the horizon).

Results

Overall densities

Egg densities were highest in the first series of tows, taken between 12 and 16 April, when mean concentration in the water column based on all nets in the tows varied from 12,057 to 34,734 eggs/1,000 m^3 (SD ranged from 5,827 to 30,619). Egg densities were greater than 1,000/1,000 m^3 per tow in series two, and generally decreased as the season progressed (Table 2). Eggs were present during series three to eight through the middle of May, but in reduced con-

Table 1

Dates and tow depths for MOCNESS series used to investigate vertical distribution of walleye pollock, *Theragra chalcogramma*, eggs and larvae in the Shelikof Strait region.

					Depths (m)															
			Day of year		Net 1		Net 2		Net 3		Net 4		Net 5		Net 6		Net 7		Net 8	
Series	Date	No. tows	Start	End	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
1	12–16 April 1987	3	102	106	1	50	50	100	100	150	150	170	170	190	190	210	210	230	230	250
2	21–27 April 1988	7	111	117	1	60	60	120	120	140	140	160	160	180	180	200	200	220	220	250
3	30 April–1 May 1988	3	120	121	1	20	20	40	40	60	60	80	80	100	100	150	150	200	200	255
4	8–11 May 1986	7	128	131	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	200
5	13–14 May 1986	3	133	134	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	180
6	15 May 1986	2	135	135	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	170
7	17–18 May 1986	2	137	138	1	15	15	30	30	45	45	60	60	80	80	100				
8	18 May 1986	1	138	138	1	15	15	30	30	45	45	60	60	80	80	100	100	150	150	195
9	23–25 May 1987	8	143	145	0	15	15	30	30	45	45	60	60	80	80	100	100	125	125	150
	Total tows	36																		

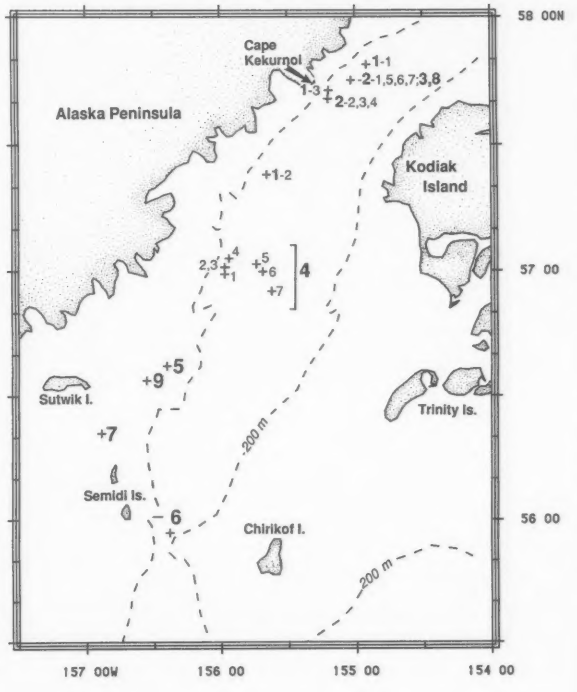


Figure 1

Locations of MOCNESS sampling series (large numbers) and tows (small numbers). Tows are shown only when there were substantial differences among their locations.

centrations, partially because sampling then was southwest of the main spawning area (Fig. 1), and partially because it was after peak spawning. The notable exception was the single tow of series eight taken in the area of maximum spawning. Although it was mid-May, egg densities were relatively high (139/1,000 m^3), indicating that some spawning had occurred within the previous two weeks.

Larvae were abundant in all series except the first when they were absent (Table 2). Mean density of larvae among the tows in series two through nine ranged from 39 to 509/1,000 m^3 (SD ranged from 54 to 1,011/1,000 m^3). Series were not always in the expected area of maximum concentration of larvae and thus do not necessarily represent the seasonal trends in larval abundance (see Kendall and Picquelle, 1990).

Series four followed a surface drifter with a drogue at 30–35 m (Incze et al., 1990), whereas sampling during series nine was at a fixed geographic location. During the 2.5 days of series four, the buoy moved anticyclonically. Catches in these two series varied considerably; during series four the mean density among tows was 82–285 larvae/1,000 m^3, compared with 42–482 larvae/1,000 m^3 during series nine (Table 2). The coefficient of variation of density among tows for series four was 0.63 and for series nine it was 0.68, indicating that variability among tows using the two sampling strategies was similar.

Overall depth distributions

Mean depths of eggs decreased during the season. Multiple comparison tests of mean depths of eggs showed significant differences between series one, two, and three, when eggs were most abundant. Among the 10 tows in the first two series, the observed mean depth of eggs was between 153 and 206 m (Fig. 2). In series three through eight, the observed mean depth was less than 130 m, but the number of eggs was relatively small. The shallower towing schemes of series four through eight may have biased the mean depth of eggs, but the general trend is thought to be real.

During the second series, when only newly hatched larvae were present, their observed mean depths of occurrence were from 165 to 212 m among tows (Fig. 3). One standard deviation of mean depth was 27 to 73 m and generally increased during the series (Fig. 3). In the third series, when recently hatched larvae dominated, larval mean depths varied from 70 to 106 m (range of SD: 83–91 m). As opposed to series two and three, when larvae were mainly found below 100 m, mean depths of larvae during series four ranged from 24 to 58 m (range of SD=15–71 m)[3]. Mean depths of occurrence of larvae from series five through seven (13–18 May 1986) varied from 15 to 47 m (range of SD=8–36 m) (Table 3). In series eight, taken in mid-May in the spawning area, the larvae averaged 4.6 mm (SD: 0.18 mm) (Table 2), and their mean depth of occurrence was 21 m (SD = 18 m). During series nine in late May, mean depths of larvae among the tows ranged from 15 to 38 m (Table 3) and varied on a diel basis (see below).

[3] Larvae in the noon tow on the second day of sampling had a mean depth of 58 m (SD=71 m). This was due to an unusually large catch in the deepest net (607/1,000 m^3 [23% of all the larvae in the tow] at 150–200 m) of larvae with a mean length of 4.71 mm. This appeared to be larger than the overall mean of the larvae collected at this depth during this series (4.35 mm), indicating the catch was not all newly hatched larvae that had not moved to the upper water column. If we discount this net, the mean depth of larvae in this tow was 21.5 m, close to the value in the other tows of the series (Fig. 4).

Changes in depth distribution with ontogeny

There was considerable variation in the mean depths of occurrence and in the abundance of eggs of different stages among the 13 tows of series one, two, and three (Table 3). Stage groups one and six were significantly deeper than stage groups three, four, and five; stage group two was intermediate in depth (Fig. 5) (ANOVA, multiple comparisons test $P<0.05$).

Almost all of the larvae collected deeper than 100 m throughout the study were <5 mm, while the length of larvae in the upper part of the water column appeared to increase later in the season (Fig. 6). In several tows of series four through eight, a bimodal depth distribution was evident; most larvae were found in the upper 60 m, almost no larvae found between 60 and 100 m, and larvae again were present deeper than 100 m. Mean lengths of larvae in the nets of the tows of series nine ranged from 4.8 to 9.8 mm, with an overall mean of 7.8 mm. There was no indication of length stratification of larvae within the upper 100 m. The mean lengths of larvae among tows in series nine were relatively homogeneous (7.2–8.6 mm).

Table 2

Mean density (number/1,000 m^3) and standard deviation (SD) of density by tow of walleye pollock, *Theragra chalcogramma*, eggs and larvae, and mean and standard deviation of larval lengths (mm SL) from MOCNESS tows.

		Density (no./1,000 m^3)					
		Eggs		Larvae		Larval length (mm SL)	
Series	Tow	Mean	SD	Mean	SD	Mean	SD
1	1	19,994	14,317.2				
1	2	12,057	5,827.0				
1	3	34,734	30,618.6				
2	1	1,509	833.3	168	271.6	3.8	0.04
2	2	3,543	3,204.0	90	89.5	3.7	0.06
2	3	2,402	1,858.9	89	90.0	3.9	0.10
2	4	1,270	804.1	230	257.8	3.8	0.06
2	5	3,641	2,489.5	322	253.2	4.1	0.04
2	6	3,276	1,696.2	389	296.1	3.6	0.04
2	7	2,333	791.3	341	316.6	3.7	0.07
3	1	411	207.6	341	444.2	4.7	0.08
3	2	671	565.3	208	163.8	4.0	0.09
3	3	779	801.3	304	331.8	4.3	0.07
4	1	52	33.4	82	88.1	5.0	0.09
4	2	77	87.1	105	130.6	4.9	0.08
4	3	98	100.7	183	288.8	4.7	0.11
4	4	124	190.6	285	449.4	5.1	0.09
4	5	170	333.2	152	228.6	5.7	0.11
4	6	204	342.4	148	199.0	5.1	0.09
4	7	59	85.0	232	261.3	5.7	0.07
5	1	26	23.7	423	696.8	5.6	0.09
5	2	40	50.2	509	770.6	5.8	0.08
5	3	24	12.9	114	121.3	5.4	0.09
6	1	5	5.0	355	497.1	6.0	0.08
6	2	7	9.1	419	833.7	6.1	0.10
7	1	14	16.1	39	58.8	6.7	0.18
7	2	5	7.7	53	91.6	6.3	0.10
8	1	139	96.7	109	184.5	4.6	0.18
9	1			42	53.5	7.7	0.50
9	2			475	822.4	7.9	0.13
9	3			181	384.8	8.6	0.16
9	4			208	482.7	7.2	0.12
9	5			78	125.1	8.2	0.17
9	6			256	385.5	7.7	0.14
9	7			482	1,011.4	7.5	0.16
9	8			396	639.5	8.5	0.11

Relationship of depth distribution and hydrography

The temperature of the water column measured concurrently with the tows in series one through three increased with depth from about 4.0° to 5.0°C near the surface to 5.0° and 5.5°C at 150–250 m, where most of the eggs occurred (there is no hydrographic data from tows 3 and 5 of series two). Temperature at the mean depth of occurrence of eggs varied from 4.7° to 5.4°C among the tows in series one through three (Fig. 7A). Since temperature increased with depth, among the tows of series one through three there was a positive linear relationship between mean depth of occurrence of eggs and temperature ($P<0.001$, $r^2=0.7619$). The relationship between the depth distribution of eggs and water density among tows of series one through three was not significant ($P=0.632$) (Fig. 7B).

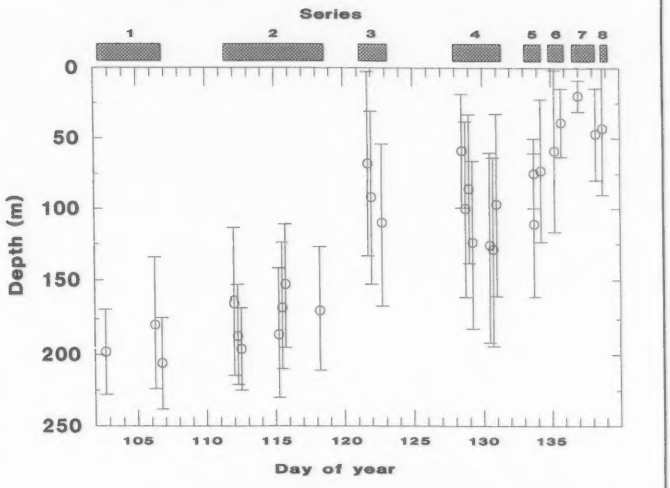


Figure 2

Eggs of walleye pollock, *Theragra chalcogramma*. Depth of occurrence by day of year and tow series number. Mean and standard deviation of the mean are shown for each tow.

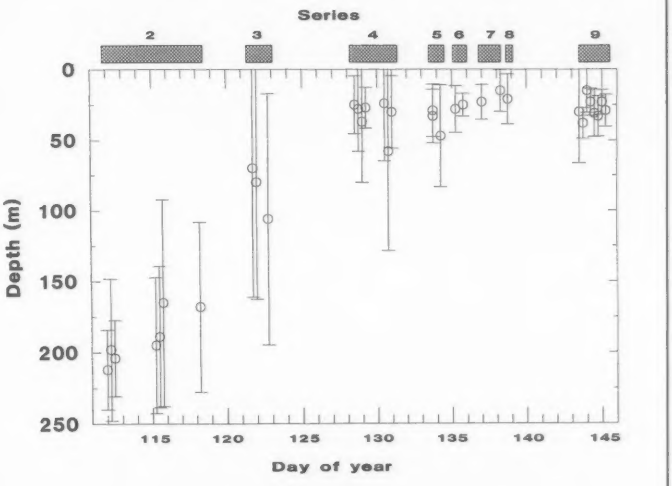


Figure 3

Larvae of walleye pollock, *Theragra chalcogramma*. Depth of occurrence by day of year and tow series number. Mean and standard deviation of the mean are shown for each tow.

When pollock larvae were first present in April as hatchlings in the lower part of the water column, they experienced temperatures of 4.9° to 5.3°C (Fig. 8). When the larvae first reached the upper part of the water column they experienced lower temperatures (~3.6°C during series four), but temperature at the mean depth of larval occurrence increased to about 5.7°C during series nine (Fig. 8).

Temperatures during series nine decreased with depth from about 6.2°C at the surface to just above

Table 3

Means and standard deviations (SD) of depths of walleye pollock, *Theragra chalcogramma*, eggs (total and by stage group) and larvae from MOCNESS tows.

				Eggs by stage group													
		Total eggs		Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Larvae	
Series	Tow	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	1	198	29.9	209	19.4	207	23.9	194	30.0	182	44.7	173	47.6	197	25.9		
1	2	179	44.8	180	31.0	174	45.6	174	51.9	183	51.2	196	51.7	200	44.9		
1	3	206	32.1	214	19.2	207	27.4	196	44.0	168	54.2	195	41.0	156	41.2		
2	1	164	50.5	161	33.2	158	48.5	156	59.6	155	54.1	158	45.7	199	42.3	212	27.9
2	2	187	33.9	179	22.4	182	27.6	193	35.1	191	36.1	184	36.5	200	35.4	198	49.8
2	3	196	28.9	196	16.9	189	24.1	191	34.7	198	31.1	199	30.1	203	30.1	204	26.6
2	4	186	44.1	177	21.9	181	25.3	163	52.0	140	65.1	177	49.2	210	33.5	195	47.6
2	5	167	43.0	206	14.2	167	36.2	143	28.8	127	38.8	144	39.4	193	34.0	189	49.5
2	6	153	42.0	193	23.2	158	47.1	145	37.3	146	37.4	143	39.7	187	40.6	165	72.7
2	7	169	42.0	184	24.9	167	31.1	159	32.6	166	49.8	159	40.1	186	46.7	168	59.7
3	1	68	65.5	144	54.6	95	66.9	54	73.3	37	40.0	56	43.6	101	77.0	70	91.1
3	2	92	60.9	133	33.4	68	52.4	84	67.8	76	46.9	92	49.1	77	67.7	80	82.7
3	3	110	55.7	84	68.8	129	56.1	94	65.5	90	47.6	102	44.8	130	51.7	106	88.9
4	1	59	40.4													25	20.5
4	2	100	61.7													28	30.1
4	3	86	52.7													37	48.3
4	4	124	57.9													27	14.5
4	5	126	65.6													24	40.9
4	6	129	65.2													58	70.5
4	7	97	64.2													30	25.7
5	1	75	24.7													29	18.6
5	2	111	50.4													33	19.0
5	3	73	50.6													47	36.2
6	1	59	57.6													28	16.5
6	2	39	24.3													25	8.0
7	1	20	11.2													23	12.3
7	2	47	32.7													15	14.8
8	1	43	47.2													21	17.7
9	1															30	36.4
9	2															38	10.9
9	3															15	15.4
9	4															23	9.6
9	5															31	16.6
9	6															33	14.3
9	7															23	8.8
9	8															29	11.3

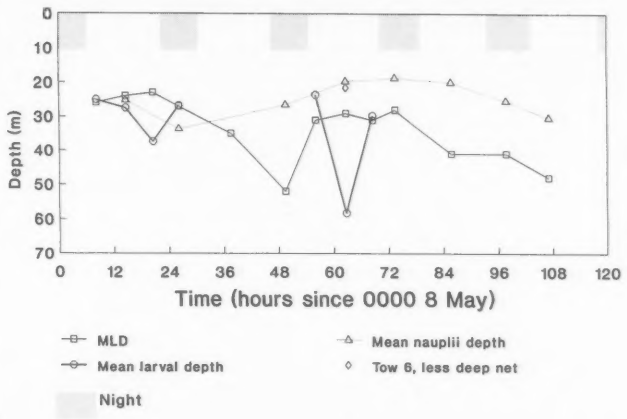


Figure 4

Time series of mixed layer depth, mean depth of copepod nauplii, and mean depth of walleye pollock, *Theragra chalcogramma*, larvae starting at 0000 hours, 8 May GMT. Mean depth of larvae excluding the catch in the deepest net of tow 6 also is plotted (see Results: overall depth distribution). Nighttime is shown by stippling near the top border.

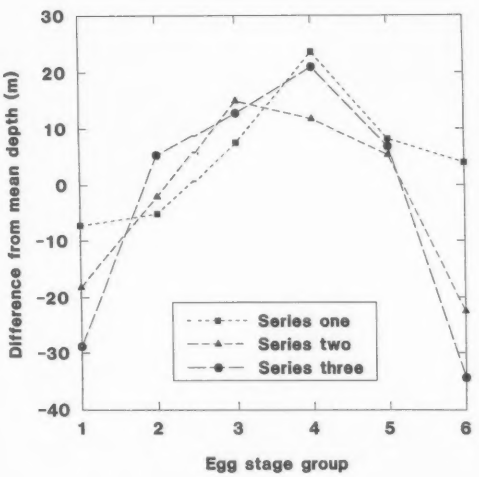


Figure 5

Vertical distribution of walleye pollock, *Theragra chalcogramma*, eggs by developmental stage group from series one, two, and three. Differences in mean depth of each stage group from mean depth of all eggs in a series are plotted.

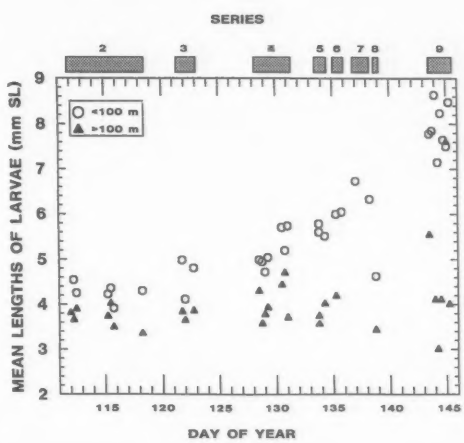


Figure 6

Standard lengths (SL) of walleye pollock, *Theragra chalcogramma*, larvae in tows above and below 100 m by day of year and tow series number.

5.0°C from about 60 m to the bottom (Fig. 9). There was a gradual thermocline between 10 and 40 m, and most of the larvae were present in or above this feature. Salinity during this series showed a gradual increase with depth from about 31.7 ppt at the surface to 32.2 ppt at 140 m. Density increased steadily from a σ_t of 24.85 at the surface to 25.25 at 60 m and 25.45 at 140 m (Fig. 9).

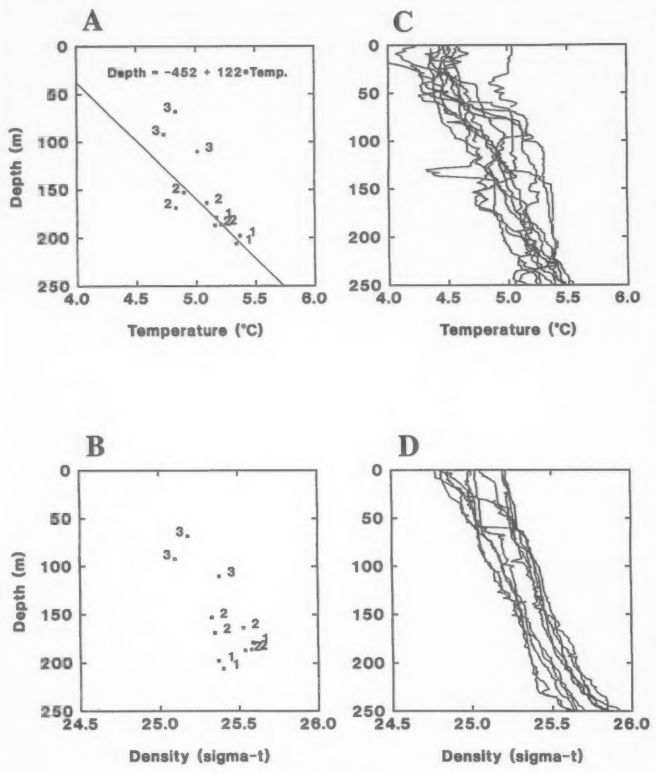


Figure 7

Mean depth of occurrence of walleye pollock, *Theragra chalcogramma*, eggs in series one, two, and three in relation to temperature (**A**) and density (**B**). Series numbers are indicated next to data points. Temperature (**C**) and density (**D**) profiles during series one, two, and three.

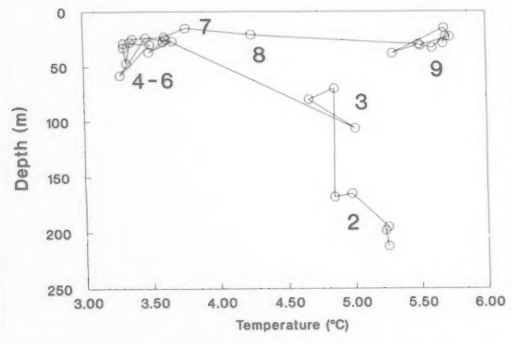


Figure 8

Mean depth of occurrence of walleye pollock, *Theragra chalcogramma*, larvae by tow in relation to temperature. Series numbers are near appropriate data points.

Diel changes in larval depth distribution

There was no clear diel pattern in the depth distribution of 5–6 mm larvae in series four (Fig. 4). During the first diel sampling period the mean depths varied from 25 to 37 m; the deepest mean depth occurred at dusk. During the second diel period, night was not sampled and an aberrant catch occurred during the noon sampling period (discussed above). The mean depths varied from 24 to 58 m, if the catch in the deep net of the noon tow is included, and from 21 to 30 m if that catch is excluded.

When proportions of larvae at each depth from series nine are examined, a clear pattern of vertical distribution emerges despite differences in overall density among tows. Although the deepest stratum sampled was 125–150 m, mean depths of occurrence of larvae were between 14.6 and 38.1 m (range of one SD=8.8–36.4 m), and fewer than 1% of all larvae were collected below 60 m. Within the upper 60 m, the larvae showed evidence of limited diel vertical migrations (Fig. 10). The observed mean depth of larvae was greater at noon than at other times (38 m and 33 m) and shallowest at dusk (15 m and 23 m). At night the larvae were found somewhat deeper (23 m and 29 m). Like the dusk sampling, the distribution at night appeared deeper during the second day compared with the first. At dawn the larvae were found between the night and noon depths (30 m and 31 m).

Although the same pattern of changes in vertical position of the larvae was observed during both 24-hour periods of series nine, differences in observed mean depths between various times of day were consistently greater on the first day than on the second (Fig. 10). The average difference in mean depth between sequential time periods on the first day was 13.2 m versus 6.2 m on the second (Table 4). The mean depths at dawn on the two days were within a meter of each other, but at the other sampling times there were differences of 4.8–8.4 m between mean depths on the two days at the same time of day. Differences were especially pronounced at dusk and night. Examination of standard deviations of mean depth and mean lengths of larvae among tows of series nine showed no consistent pattern of differences with any of the variables under consideration (time of day, depth, day).

Response of larvae to wind events and prey distributions

Increasing winds after 60 hours of sampling during series four prevented further MOCNESS tows, but other observations continued during the storm and documented the deepening of the mixed layer and subsequent changes in microzooplankton distribution (Incze et al., 1990). The path of the drogue, the sequence of CTD data obtained in the area, and limited satellite imagery suggested the presence of an anticyclonic eddy (Incze et al., 1990; Nieman[4]). The mixed layer depth during the first half of series four was variable, but during the last half it deepened, presumably in response to increased winds (Fig. 4). Copepod nauplii of length range 150–350 μm, which has been found to be the size range primarily eaten by 5–6 mm walleye pollock larvae (Paul et al., 1991), had mean depths between 20 and 34 m during series four (Fig. 4). Their observed mean depth increased during the storm, but their densities at some depth within the upper 45 m was always greater than 15 per liter. Excluding the deep net from the noon tow on day two, the mean depths of larvae in series four were at or 5–10 m below the mixed layer depth and the mean depth of 150–350 μm copepod nauplii.

Wind, measured hourly aboard the ship during series nine, increased from less than 8 m/second during the first six tows of this series to over 12 m/second by the end of the series. The mixed layer was about 25 m deep at the time of the last tow (night) in series nine as opposed to about 10 m during the previous seven tows (Fig. 9). The greater mean depths of larvae at dusk and night on the second day of sampling compared with the first day of sampling were possibly caused by increased turbulence and deepening of the mixed layer (Fig. 10).

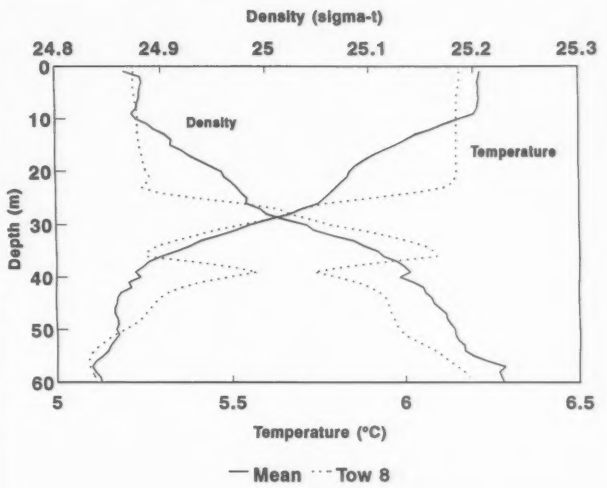


Figure 9

Temperature and density profiles from series nine. Profiles of means of all tows and from tow eight, showing deepening of the mixed layer (see Results: response of larvae to wind events and prey distributions), are plotted.

Table 4

Comparisons (means and standard deviations [SD]) of walleye pollock, *Theragra chalcogramma*, larvae by depth (m), length (mm SL) and density (no./1,000 m^3) in series nine at four times of day (dawn, noon, dusk, and night).

		Depth (m)		Length (mm SL)		Density (no./1,000 m^3)	
Tow	Time	Mean	SD	Mean	SD	Mean	SD
1	dawn	30	36.4	7.7	0.50	42	54
2	noon	38	10.9	7.9	0.13	475	822
3	dusk	15	15.4	8.6	0.16	181	385
4	night	23	9.6	7.2	0.12	208	483
5	dawn	31	16.6	8.2	0.17	78	125
6	noon	33	14.3	7.7	0.14	256	386
7	dusk	23	8.8	7.5	0.17	482	1,011
8	night	29	11.3	8.5	0.11	396	640
	dawn	30.6		8.06		33.6	
	noon	36.6		7.79		249.6	
	dusk	21.4		7.72		228.4	
	night	27.0		8.09		150.7	
	day 1	26.4		7.84		124.9	
	day 2	29.0		7.97		156.2	

Discussion

Most walleye pollock eggs in Shelikof Strait developed at depths between 150 and 200 m. However, there was considerable variation in the mean depth of eggs among the tows. Mean depth of eggs varied from 153 to 206 m in April (when egg densities were high) and from 20 to 129 m in

[4] Nieman, D. R. Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, Miami, Florida 33149. Personal commun., February 1993.

May. Although many factors probably contributed to the distribution of eggs, their distribution was positively related to temperature, which increased with depth.

Kendall and Kim (1989) developed a model, based on field collections and laboratory experiments, to describe the vertical distribution of walleye pollock eggs from Shelikof Strait in relation to water density. One of the model's assumptions was that the specific gravity of eggs does not vary interannually. Based on this assumption and their observations of the changes in egg buoyancy and depth distribution during development, eggs would rise to different depths in the middle stages of development depending on water density in particular years. The vertical distribution might then influence the horizontal distribution of eggs if there was a significant vertical shear in the water column. Like Kendall and Kim (1989), we found middle-stage pollock eggs at shallower depths than early or late stage eggs. Our data, however, suggest that the depth distribution of eggs changes during development regardless of water density. Pollock egg density appears to vary interannually—in the eight tows from which significant numbers of eggs were collected and for which concurrent hydrographic data are available, the mean depth of occurrence varied from 153 to 206 m, and the density varied from 25.31 σ_t to 25.63 σ_t. Among the four years for which Kendall and Kim (1989) present data (1977, 1981, 1985, 1986), density in the middle layer of the water column (162–216 m) varied interannually from 25.58 σ_t to 25.87 σ_t, and modelled depth distribution of middle-stage eggs varied from about 160 to 230 m. While the ranges of density and depth of eggs seen in the present study are similar to those modelled by Kendall and Kim (1989), the proposed relationship between depth of eggs and water density is not evident. A relationship might have been seen if a greater range of water densities had been found. The temperature and density of the water in which most of the eggs were found in the present study (1987 and 1988) most closely resembled the values reported for 1981 by Kendall and Kim (1989).

Ingraham et al. (1991) compared long-term annual means of water temperature, salinity, and density at 225 m depth in Shelikof Strait with values in individual years when circulation in the Gulf of Alaska was anomalous. They found high values for all three variables in 1985; this was a year when water on the continental slope did not include fresher, colder waters from the eastern Gulf of Alaska owing to reduced westward transport. Of the years considered here (1985–88), only 1985 was characterized by anomalous flow conditions that could have produced unusually warm, dense (>5.4°C, >26.2 σ_t) bottom water in Shelikof Strait (Ingraham et al., 1991). According to the model in Kendall and Kim (1989), the eggs should have risen closest to the surface in 1985. However, mean depth of eggs in the four tows in 1985 was 220 m, in the five tows in 1986 it was 211 m (Kendall and Kim, 1989), in the three tows of series one in 1987 it was 200 m, and in the seven tows of series two in 1988 it was 176 m.

In series three through eight, the mean depth of occurrence of eggs was less than 130 m. Given the low numbers of eggs and the sampling intervals designed mainly to sample larvae, these values are not robust. Kendall and Kim (1989) also found some eggs with significantly lower density than others in their specific gravity experiments. The data presented here confirm that some eggs have a low specific gravity value, but that these are infrequent and occur primarily later in the season after the majority of eggs have hatched.

Apparently after hatching, larvae move quickly to the upper part of the water column. Both eggs and larvae in series two had mean depths of occurrence between 153 and 212 m among the seven tows. The mean length of larvae in series two was 3.8 mm, which is within the range of size at hatching (Kendall

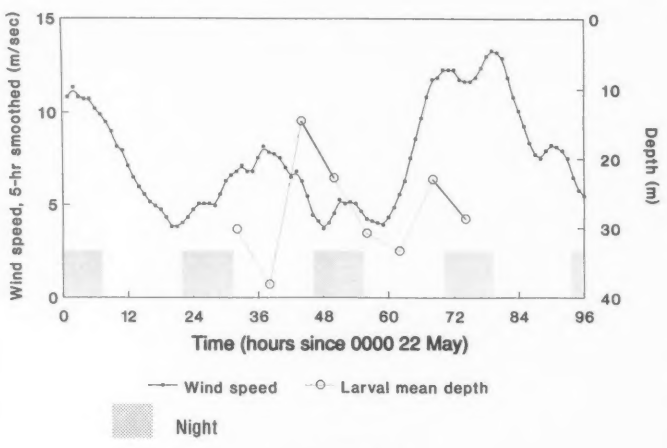


Figure 10

Mean depth of walleye pollock, *Theragra chalcogramma*, larvae and wind speed during series nine.

et al., 1987). In series three, the mean depths of occurrence of eggs and larvae decreased to between 68 and 110 m, and the mean length of larvae increased to 4.4 mm, indicating that growth of some pollock larvae had occurred (SD of length was 0.18 in series three as opposed to 0.09 in series two). The standard deviations of depth of larval occurrence in series three (83 to 91 m) were larger than in any other series, suggesting that these larvae were in transition from the deep hatching environment to shallower levels. Although larvae respond positively to light within 24 hours of hatching, their negative geo/barotaxis may enable them to reach the upper layers since insufficient light for response penetrates to hatching depths (see Olla and Davis, 1990). The relatively shallow mean depth of eggs in series three also may account for the large variation in larval depth during that series. Older larvae from eggs at the depths observed during series two (>150 m) could have mixed with larvae hatching from eggs found at the depths observed during series three (<110 m). The larger standard deviation of larval length in series three compared with series two supports this explanation. In later series the mean depth of occurrence of the larvae was less than 60 m, and the standard deviation generally was less than 20 m. Once they reach the upper layers, vertical movements increase as larvae develop. No significant diel migrations were noted in series four, as opposed to the pattern seen in series nine. The mean length of larvae in series four was 5.3 mm; in series nine it was 7.9 mm. The larvae sampled by Kendall et al. (1987) in late May were 11.0 mm long and demonstrated a pattern of vertical distribution similar to the larvae collected here in series nine.

During series nine, larvae followed a diel (crepuscular) pattern of vertical movements in which they ranged deepest at noon, shallowest at dusk, and progressively deeper through the following noon. Although this pattern was observed on both days, the amplitude of movements were reduced on the second day. However, the wind had markedly increased by evening of the second day. Larvae may have been avoiding the turbulent surface on the second day when their mean depths were deeper. Olla and Davis (1990) found that pollock larvae avoid turbulence in the laboratory.

The relationships of larval fish feeding, growth, and survival to storms and turbulence have been the subject of numerous studies (e.g. see Sundby and Fossum, 1990; Maillet and Checkley, 1991). Both positive and negative effects have been postulated and observed. Positive effects of increased turbulence include hypothesized enhanced encounter rates between larvae and their prey (Rothschild and Osborn, 1988), and enhanced primary production after mixing has ceased owing to infusion of nutrients from below the photic zone. Negative impacts include dilution of vertically enriched layers of prey to levels below successful feeding thresholds and reduced naupliar production in lower phytoplankton concentrations (Lasker, 1978). There is evidence that in Shelikof Strait, below-average walleye pollock production may result if strong wind events occur when larvae are at the first-feeding stage.[5] Incze et al. (1990) found that naupliar concentrations remained above feeding threshold levels during the passage of a storm, but this was a relatively transient phenomenon. The present study indicates that larvae may avoid upper layer turbulence by moving deeper in the water column. If so, they might experience prey densities or light levels too low for optimal feeding.

In a 24-hour study of the vertical distribution of pollock larvae in Auke Bay, Alaska (average depth 60 m), Pritchett and Haldorson (1989) found larvae congregated at 10 m at noon, at 5 m at dawn and afternoon, and at 15–20 m at night. At twilight (0.3 hour before sunrise, 1.5 hours before sunset), larvae were more dispersed, seen mostly at 10 m near sunrise and at 15 m near sunset. The vertical extent of diel migration increased with larval length. In the present study, depths of occurrence were greater at all times than those reported by Pritchett and Haldorson (1989), and noon depths of larger larvae were greater than the night depths. However, in both studies, larvae were found to be deeper at noon than at dawn and dusk, and a relationship between vertical migration and larval length was seen. The depth distribution of copepod nauplii in Auke Bay usually centered around 5–10 m (Paul et al., 1991). Inzce et al. (1990) reported maximum densities of copepod nauplii in the upper 30 m of Shelikof Strait when pollock larvae are abundant. Since nauplii are the primary prey for pollock larvae, the larvae may well adjust their daytime feeding depths to correspond to those of the nauplii. Alternatively, the greater daytime depth of pollock larvae in Shelikof Strait may be related to the greater depth of light penetration in Shelikof Strait compared with Auke Bay (Zeimann et al., 1990).

Light is frequently cited as a factor controlling the depth of occurrence for fish larvae. Larvae of some species follow the common trend of rising toward the surface at night and of remaining deeper during the day (Smith et al., 1978; Kendall and Naplin, 1981; Davis et al., 1990). Other species follow an opposite pattern, ranging deeper at night than by day (Boeh-

[5] Bailey, K. M., AFSC, and S. A. Macklin, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE., Seattle, Washington 98115-0070. Personal commun., February 1993.

lert et al., 1985; Yamashita et al., 1985; Sogard et al., 1987; Davis et al., 1990). Fewer studies have examined the vertical distribution of fish larvae during crepuscular periods. The present study has shown that larger larval pollock range deeper during the day than at night and that, at dawn and dusk, they are present at shallower depths in the water column than at midday. We hypothesize that these changes in vertical position allow pollock larvae to extend the length of their daily feeding period.

In the laboratory, first-feeding pollock larvae could not feed at light levels below 0.006 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Paul, 1983). Except at night, light levels are brighter than those at the depths where we found feeding-stage larvae. In studies of behavioral responses of walleye pollock larvae (4–8 mm SL) to light in the laboratory, Olla and Davis (1990) found reduced activity and orientation in a nonfeeding mode at light levels <0.01 and avoidance of light at levels >13 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In the dark, larvae migrated upward and remained in the upper part of the chambers, demonstrating negative geotaxis or barotaxis, or both. Light levels between 0.01 and 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are estimated to have occurred between about 25 and 60 m during our sampling in Shelikof Strait. The mean depths of feeding larvae were typically in the upper part of this range (Fig. 11). Larvae longer than 7 mm seemed to adjust their vertical position on a diel cycle to stay at light levels similar to those "preferred" in the laboratory. At night these larvae were present at depths where light had been greater than 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the day.

The relationship of vertical distribution of larval fish to vertical temperature structure of the water column varies among species (Kendall and Naplin, 1981; Sogard et al., 1987). Hypothetically, there are metabolic advantages to diel descents into cooler waters (Lampert, 1989). Larvae that stay nearer the surface (at higher temperatures) at night when they are digesting their food may accrue such advantages (Wurtsburgh and Neverman, 1988). However, given the small differences in temperature with depth observed here (~1°C), energetic advantages are almost certainly insignificant compared with the advantages of feeding at optimal light levels and at depths of maximum prey abundance. An alternative advantage of residing deeper, and thus at lower light levels during daytime, may be to avoid visual predators.

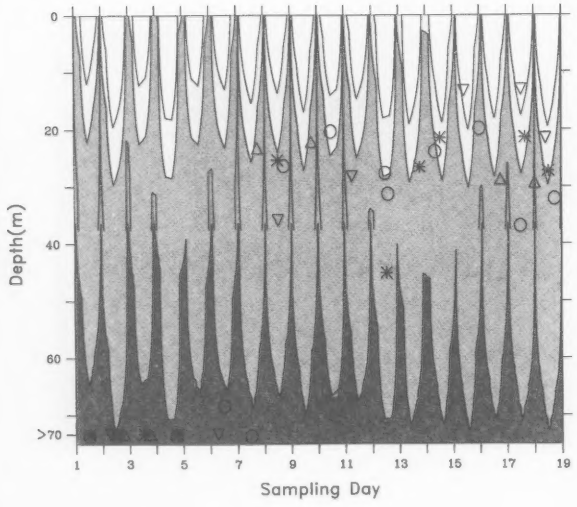


Figure 11

Predicted light levels at depth on days of sampling and mean depths of walleye pollock, *Theragra chalcogramma*, larvae in MOCNESS tows (indicated by circles for daytime tows, triangles pointed down for dusk tows, asterisks for night tows, and triangles pointed up for dawn tows). Depths of three light levels are plotted: 50, 10 and 0.01 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Light levels above 50 are clear, those 10–50 are light gray, those 0.01–10 are medium gray, and those less than 0.01 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are dark gray. Light levels are based on incident light at the Kodiak airport during the sampling periods with an extinction coefficient of 0.16.

Acknowledgments

Many people, mainly from the AFSC, helped collect and process the samples and data upon which this paper is based. We thank them all, particularly those who endured the harsh conditions of Shelikof Strait during the cruises there. David Nieman rendered his expert help in operating the MOCNESS on several cruises. Allen Macklin (PMEL) is thanked for obtaining and analyzing meteorological data presented here. Richard Davis (AFSC) graciously let us use irradiance with depth data obtained by his modelling efforts. An earlier draft of the manuscript was helped immeasurably by reviews of many of the researchers involved in the FOCI (Fisheries-Oceanography Coordinated Investigations) program: Kevin Bailey, Jim Schumacher, Jeff Napp, Ric Brodeur, Bori Olla, Gary Stauffer, and Susan Picquelle (whom also aided in statistical analyses). Ian Perry (Canada, Department of Fisheries and Oceans) also provided a very helpful review of the manuscript.

Literature cited

Ahlstrom, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull. 60:107–146.

Blood, D. B., A. C. Matarese, and M. M. Yoklavich.
1994. Embryonic development of walleye pollock, *Theragra chalcogramma,* from Shelikof Strait, Gulf of Alaska. Fish. Bull. 92:207–222.

Boehlert, G. W., D. M. Gadomski, and B. C. Mundy.
1985. Vertical distribution of ichthyoplankton off the Oregon Coast in spring and summer months. Fish. Bull. 83:611–621.

Coombs, S. H., R. K. Pipe, and C. E. Mitchell.
1981. The vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) in the eastern North Atlantic and North Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:188–195.

Davis, T. L. O., G. P. Jenkins, and J. W. Young.
1990. Diel patterns of vertical distribution in larvae of southern bluefin *Thunnus maccoyii* and other tuna in the East Indian Ocean. Mar. Ecol. Prog. Ser. 59:63–74.

Ellertson, B., P. Solemdal, S. Sundby, S. Tilseth, T. Westgard, and V. Oiestad.
1981. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:317–319.

Enright, J. T.
1977. Diurnal vertical migration: adaptive significance and timing. Part 1: Selective advantage: a metabolic model. Limnol. Ocean. 22:856–872.

Hardy, A. C.
1936. Plankton ecology and the hypothesis of animal exclusion. Proc. Linn. Soc. Lond. 148:64–70.

Ingraham, W. J., Jr., R. K. Reed, J. D. Schumacher, and S. A. Macklin.
1991. Circulation variability in the Gulf of Alaska. EOS, Trans. Am. Geophys. Soc. 74:257–264.

Incze, L. S., J. Gray, J. D. Schumacher, A. W. Kendall Jr., K. M. Bailey, and S. A. Macklin.
1987. Fisheries-Oceanography Coordinated Investigations (FOCI) field operations—1986. NOAA Data Report ERL PMEL-20, 64 p.

Incze, L. S., P. B. Ortner, and J. D. Schumacher.
1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12:365–379.

Kamba, M.
1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay, Hokkaido. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175–197.

Kendall, A. W., Jr., and N. A. Naplin.
1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fish. Bull. 79:705–726.

Kendall, A. W., Jr., and S. Kim.
1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 169–180. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Kendall, A. W., Jr., and S. J. Picquelle.
1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish Bull. 88:133–154.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Lampert, W. H.
1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3:21–27.

Lasker, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:212–230.

Lawrence, L. A., J. Gray, and J. D. Schumacher.
1991. Fisheries-Oceanography Coordinated Investigations field operations—1987. NOAA Data Rep. ERL PMEL-28, 61 p.

Lough, R. G., and D. C. Potter.
1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fish Bull. 91:281–303.

Maillet, G. L., and D. M. Checkley Jr.
1991. Storm-related variation in growth rate of otoliths of larval Atlantic menhaden *Brevoortia tyrannus*: a time series analysis of biological and physical variables and implications for larva growth and mortality. Mar. Ecol. Prog. Ser. 79:1–16.

Munk, P., T. Kiorboe, and V. Christensen.
1989. Vertical distribution of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environ. Biol. Fish. 26:87–96.

Neilson, J. D., and R. I. Perry.
1990. Diel vertical migrations of marine fishes: an obligate or facultative process? Adv. Mar. Biol. 26:115–168.

Norcross, B. L., and R. F. Shaw.
1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am. Fish. Soc. 113:153–165.

Olla, B. L., and M. W. Davis.
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105–112.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae, *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Paul, A. J., K. O. Coyle, and L. Haldorson.
1991. Interannual variations in copepod nauplii prey of larval fish in an Alaskan Bay. ICES J. Mar. Sci. 48:157–165.

Pritchett, M., and L. Haldorson.
1989. Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*). *In* Proceedings of the international symposium on the biology and management of walleye pollock; 14–16 November 1988, Anchorage, AK, p. 173–183. Alaska Sea Grant Rep. 89–1, Univ. Alaska, Fairbanks.

Proctor, P. D.
1989. Fisheries-Oceanography Coordinated Investigations—field operations 1988. NOAA Data Report ERL PMEL-25, 69 p.

Rothschild, B. J., and T. R. Osborn.
1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10:465–474.

Scheaffer, R. L., W. Mendenhall, and L. Ott.
1986. Elementary survey sampling. Duxbury Press, Boston, MA, 324 p.

Schumacher, J. D., and A. W. Kendall Jr.
1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. CalCOFI Rep. 32:22–40.

Sclafani, M., C. T. Taggart, and K. R. Thompson.
1993. Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. J. Plankton Res. 15:413–435.

Smith, W. G., J. D. Sibunka, and A. Wells.
1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. Fish. Bull. 76:167–178.

Sogard, S. M., D. E. Hoss, and J. J. Govoni.
1987. Density and depth distribution of larval Gulf menhaden, *Brevoortia patronus*, Atlantic croaker, *Micropogonias undulatus*, and spot, *Leiostomus xanthurus*, in the northern Gulf of Mexico. Fish. Bull. 85:601–609.

Sundby, S., and P. Fossum.
1990. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. J. Plankton Res. 12:1153–1162.

Weibe, P. D., K. H. Burt, S. H. Boyd, and A. W. Morton.
1976. A multiple opening/closing net and environmental sensing system for zooplankton. J. Mar. Res. 34:313–326.

Wurtsburgh, W. A., and D. Neverman.
1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333:846–848.

Yamashita, Y., D. Kitagawa, and T. Aoyama.
1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel *Ammodytes personatus*. Bull. Japan. Soc. Sci. Fish. 51:1–5.

Zeiman, D. A., L. D. Conquest, K. W. Fulton-Bennett, and P. K. Bienfange.
1990. Interannual variability in the physical environment of Auke Bay, Alaska. *In* D. A. Ziemann and K. W. Fulton-Bennett (eds.), APPRISE-interannual variability and fisheries recruitment, p. 99–128. The Oceanic Institute, Honolulu, HI.

A comparison of a validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional scale method

Susan K. Lowerre-Barbieri

Virginia Institute of Marine Science, College of William and Mary
Gloucester Point, Virginia 23062
Present address: University of Georgia Marine Institute
Sapelo Island, Georgia 31327

Mark E. Chittenden Jr.

Virginia Institute of Marine Science, College of William and Mary
Gloucester Point, Virginia 23062

Cynthia M. Jones

Applied Marine Research Laboratory, Old Dominion University
Norfolk, Virginia 23529

Abstract.—Otoliths, scales, dorsal spines, and pectoral-fin rays were compared to ascertain the best hardpart for determining the age of weakfish, *Cynoscion regalis*. Each showed concentric marks, which could be interpreted as annuli. Sectioned otoliths, however, consistently showed the clearest marks, had 100% agreement between and within readers, and were validated by the marginal increment method for ages 1–5. This validated method of ageing weakfish was then compared with the traditionally used scale method. The scale method was less precise, as demonstrated by lower percent agreement, and generally assigned younger ages for fish older than age 6 (as determined by otoliths). Consequently, mean sizes at age based on scales showed no clear signs of an asymptote, whereas those based on otoliths did. Otolith annuli formed in April and May, whereas scale annulus formation was more variable, ranging from April to August. This extended time of annulus formation made scales poorly suited for back calculation.

The weakfish, *Cynoscion regalis*, is a recreationally and commercially important sciaenid found from eastern Florida to Massachusetts, and is most abundant from North Carolina to New York (Mercer, 1985). Believed to be resident year-round in the Carolinas, they are found farther north only seasonally (Bigelow and Schroeder, 1953). In the spring, weakfish migrate northward and inshore to estuarine feeding and spawning grounds; this pattern is reversed in the fall (Wilk, 1979). Most fish are believed to overwinter off North Carolina (Pearson, 1932). Weakfish are found in Chesapeake Bay, roughly from April through November (Pearson, 1941; Massmann et al., 1958), where they support one of the region's most important fisheries (Rothschild et al., 1981).

Weakfish age and growth studies have been based almost exclusively on scales (Taylor, 1916; Nesbit, 1954; Perlmutter et al., 1956; Massmann, 1963a; Merriner, 1973; Shepherd and Grimes, 1983). However, problems with this method have been reported: 1) small fish may not lay down a first annulus on scales (Welsh and Breder, 1923), 2) older fish have closely spaced annuli that are difficult to interpret (Taylor, 1916; Shepherd, 1988), 3) annuli form over a long time period, April–August, and scales are difficult to interpret during annulus formation (Nesbit, 1954; Massmann, 1963b), 4) the time annuli form varies annually and regionally (Perlmutter et al., 1956), and 5) checks (false annuli) and regenerated scales are common (Merriner, 1973). The scale method of ageing weakfish also has not been conclusively validated by current standards (Beamish and McFarlane, 1983; Brothers, 1983). Perlmutter et al. (1956) and Shepherd and Grimes (1983) both tried to validate annuli on scales by the marginal increment method, however they used pooled age data and did not report the age range.

Manuscript accepted 8 November 1993.
Fishery Bulletin 92:555–568 (1994).

Contribution 1826 from the College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

Although recent studies have shown that for many species the scale method underages older fish at the point where fish growth becomes asymptotic (Beamish and Chilton, 1981; Beamish and McFarlane, 1983; Barnes and Power, 1984), there has been little evaluation of other weakfish hardparts. Merriner (1973) compared weakfish scales to whole vertebrae and otoliths, and Villoso (1989) compared scales to whole otoliths. Both concluded that scales were best. However, Merriner's study was conducted before thin-sectioning of otoliths (Williams and Bedford, 1974; Beamish, 1979; Beamish and Chilton, 1981) and other hardparts became common and Villoso (1989) did not consider thin-sectioning.

A decline in weakfish landings since 1980, coupled with greater competition between fisheries, caused the Atlantic States Marine Fisheries Commission (ASMFC) to develop a weakfish management plan in 1985 (Mercer, 1985). Since then the ASMFC has issued an updated stock assessment[1] and suggested a 25% reduction in coast-wide exploitation rates (Amendment No. 1 of the Weakfish Fishery Management Plan of the ASMFC). However, it is essential to proper weakfish management that a validated ageing technique be developed and used, as improper ageing can lead to faulty estimates of model parameters such as age at maturity, growth, longevity and mortality (Beamish and McFarlane, 1983).

The objectives of this study were 1) to compare otolith, dorsal-fin spine, and pectoral-fin ray sections with scales in terms of legibility and interpretation of potential annual marks, ease of collection and processing, and precision, 2) to validate the hardpart demonstrating the greatest clarity by marginal increment analysis for each age group found in the Chesapeake Bay area, and 3) to conduct a more in-depth comparison of the validated hardpart with scales in terms of precision and accuracy, time of annulus formation, growth estimates, and use in back calculation of body length.

Methods

Preliminary comparison of hardparts

Four hundred weakfish were collected every other week during April–October in 1989 from three Chesapeake Bay commercial pound nets. On each collection day, one 22.7 kg (50 lb) box of each available grade of weakfish—small, medium, or large—was bought and all fish within it processed. Fish were measured for total length (TL ±1.0 mm), sexed, and both sagittal otoliths were removed and stored dry. Scales were removed from an area just posterior to the tip of the left pectoral fin, below the lateral line. The left pectoral fin and the entire dorsal fin were removed by cutting below the base of the rays. Scales and fins were stored in paper envelopes and kept frozen until preparation for ageing.

A total of 45 fish, 15 from each grade, were randomly selected from the fish collected in 1989 for a preliminary comparison of hardparts. These fish ranged from 244 to 615 mm TL and each of their four hardparts was prepared for reading as described below.

The right otolith from each fish was transversely sectioned through the nucleus with a Buehler low-speed Isomet saw. Sections 350–500 μm thick were mounted on glass slides with Flo-Texx clear mounting medium and viewed under a dissecting microscope at 24× magnification by using transmitted light and bright field, with the exception of samples from the period April–May, when sections were also read with reflected light and dark field to help identify the last annulus. Thin opaque bands, presumed to represent annual marks, were counted along the otolith sulcal groove (Fig. 1). Because opaque bands inhibit light passage, they appeared dark in transmitted light (Fig. 2A) and light in reflected light.

Scales from each fish were soaked in water until soft, after which they were washed gently with a soft-bristled tooth brush. Three or four clean, unregenerated scales

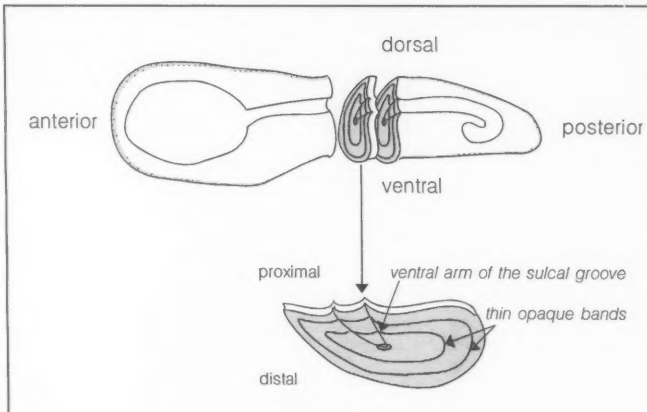


Figure 1

Schematic representation of a transverse section taken through the right sagittal otolith. The ventral arm of the sulcal groove, along which otoliths were measured, is indicated. The whole otolith is positioned as it would be in a weakfish, *Cynoscion regalis*.

[1] Vaughan, D. S., R. J. Seagraves, and K. West. 1991. An assessment of the Atlantic weakfish stock, 1982–1988. Atl. States Mar. Fish. Comm. Spec. Rep. 21, Wash. DC, 29 p.

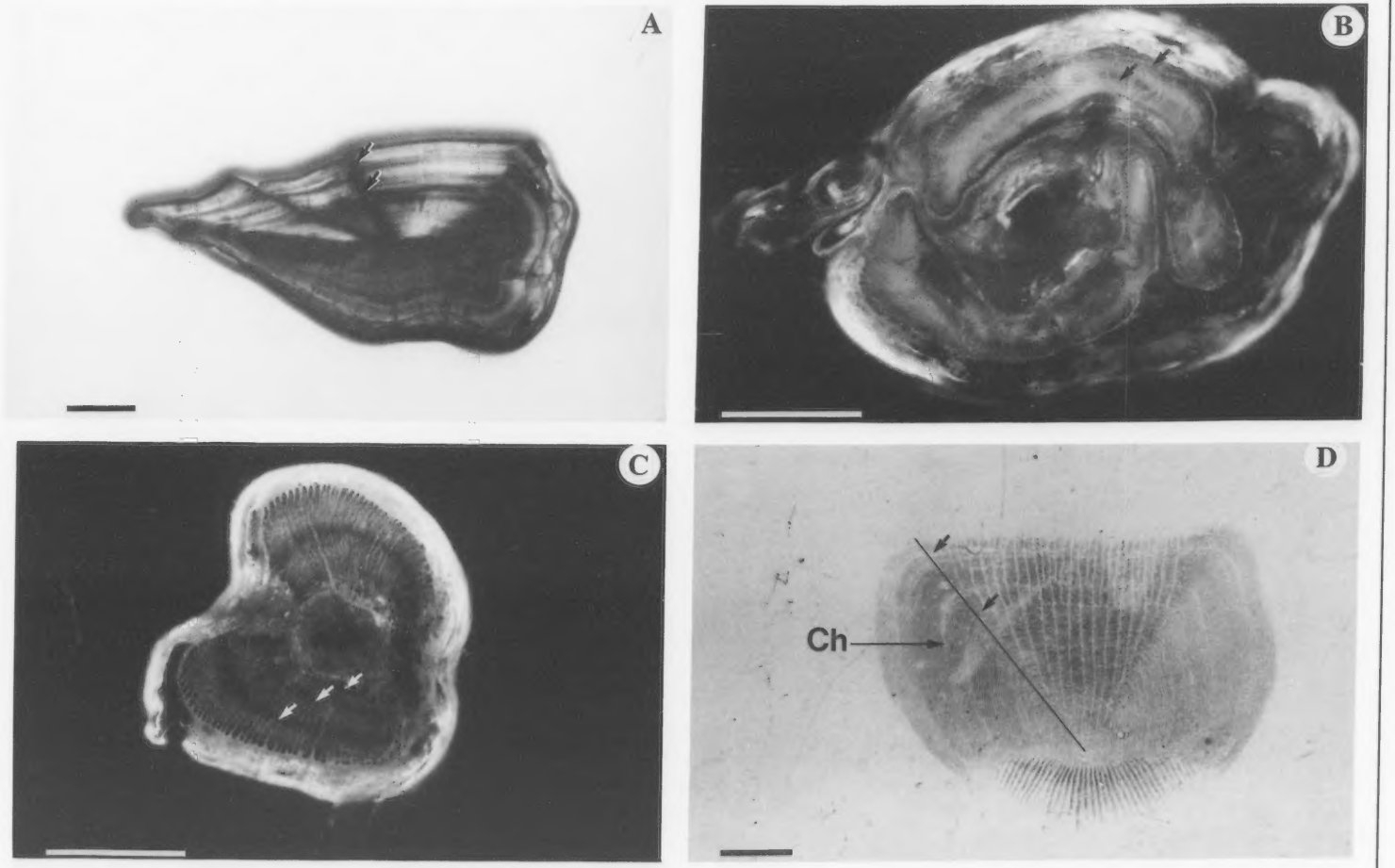


Figure 2

Marks on hardparts taken from a two-year-old (as aged by otoliths) female weakfish, *Cynoscion regalis*, TL=392 mm, collected in mid-September. (**A**) otolith section, as seen in transmitted light, bar=1 mm; (**B**) pectoral ray section, as seen in transmitted light and dark field, bar=0.5 mm; (**C**) dorsal spine section, as seen in transmitted light and dark field, bar=0.5 mm; and (**D**) scale impression, as seen in transmitted light, bar=1 mm. The left radius, which was the scale measuring axis, is marked. Ch=check. Arrows indicate individual marks counted.

were then dried, taped to an acetate sheet, inserted between two other blank sheets, and pressed with a Carver laboratory scale press for two minutes at 2,721 kg of pressure at 71°F. Because of the large size of weakfish scales, scale impressions were read with a standard microfiche reader at 20×. Those scales with potential annuli crowded along the scale periphery were also viewed at 48× under a dissecting microscope. Presumed annual marks were identified by standard criteria (Bagenal and Tesch, 1978; Shepherd, 1988).

One spiny ray from the dorsal fin and one soft ray of the left pectoral fin were prepared from each fish. Rays were serially sectioned by starting at their base and cutting through most of their length at a thickness of 400 µm with a Buehler low-speed Isomet saw. Sections were then mounted on microscope slides with Flo-Texx and read under a dissecting microscope with transmitted light and dark field at 64×. Presumed annual marks were counted when they could be identified as individual, opaque bands.

Each hardpart was read twice by two separate readers. Readings were done in a randomly selected order, with no knowledge of collection date or fish size. Hardparts were evaluated in terms of clarity of presumed annual marks, ease of collection and processing, and precision. Precision was measured by average percent agreement within and between readers, i.e. percent agreement within readers was calculated for each reader separately and then averaged for the two readers and percent agreement between readers was calculated separately for each reading and then averaged for the two readings.

Validation of the otolith method

Because otoliths were found best for ageing, additional samples were collected for validation. During 1989–92, 1,928 weakfish were collected from commercial pound-net, haul-seine, and gill-net fisheries in Chesapeake Bay. During March–November when weakfish are not present in the Chesapeake Bay, fish were collected (n=289) from the trawl fishery operating in North Carolina shelf waters north of Cape Hatteras.

The marginal increment method was used to validate otolith annuli (Brothers, 1983; Casselman, 1987; Hyndes et al., 1992). The translucent margin outside the proximal end of the last annulus was measured along the ventral side of the otolith sulcal groove (Fig. 1). Measurements were taken with an ocular micrometer to the nearest 0.038 mm (one micrometer unit at a total magnification of 24×).

Comparison of scales and otoliths

To compare the otolith and scale methods in more detail, 155 fish ranging from 140 to 845 mm TL were selected by stratified, random subsampling—strata being otolith-determined ages—from a total of 300 fish collected in 1989 and 1992. Thirty fish were selected from each of the age-strata, 1–4. Because older fish were scarce, only 14 age-5, 16 age-6, two age-7, two age-8, and one age-10 fish were included. Although most fish came from Chesapeake Bay commercial fisheries, in order to increase the number of older fish, 27 fish were collected in May 1992 at the Delaware Bay Weakfish Sport Fishing Tournament. We collected an additional 20 fish in August 1992 to include fish from each of the summer months for marginal increment and back-calculation analyses.

Hardparts were prepared as described for the preliminary comparison and read twice by each of two readers. An effort was made to determine annuli on scales based only on physical criteria and not to assign annuli based on any preconceived ideas of growth (Casselman, 1983). Reading order was randomized and collection date and fish size were unknown. Each reader recorded the number of presumed annuli and a "+" if there was growth beyond the last annulus or a "*" if the last presumed annulus was forming or had just formed (Casselman, 1987). After all hardparts had been read, we assigned ages using a January 1 birthdate, knowledge of the time of annulus formation, the relative growth of the hardpart margin, and date of capture.

Variability within reader, between readers, and between hardparts was analyzed by percent agreement. When an individual reader's counts of presumed annuli disagreed, a third reading was made. When readers' ages disagreed, a third reading with both readers present was made to resolve the disagreement.

To compare time of annulus formation and its variability in scales and otoliths, mean monthly relative marginal increments and their ranges were calculated and plotted (April–October). Relative marginal increments were calculated by dividing the marginal increment by the hardpart radius. All ages were pooled. Additionally, those hardparts which had been designated as having an annulus on the margin ("*") were reviewed and their time of collection recorded.

To determine marginal increments and to conduct back-calculation analyses, hardparts were measured by using a Via 100 camera/monitor system with a dissecting microscope at 24×. Otolith radius (OR) and otolith annular radius (OAR)—the distance from the nucleus to the proximal edge of each annulus—were measured along the ventral arm of the sulcal groove. Scale radius (SR) and scale annular radius (SAR) were measured along the left radius (Ricker, 1992). Marginal growth was measured from outside the last annulus to the hardpart edge.

To evaluate the applicability of scales and otoliths for back-calculation, it was necessary to first analyze separately their total length to hardpart relationships. Seasonal effects were assessed by comparing hardpart size of one age class taken from different seasons to that predicted by the linear regression of total length on hardpart size for all fish. Only one age class (age 3) was used to remove any confounding effects of age. This age class was chosen because it was well-represented throughout the seasons.

Back-calculation relationships for both scales and otoliths were based on the "body proportional" hypothesis (Francis, 1990) proposed by Whitney and Carlander (1956):

$$L_i = [g(S_i) / g(S_c)] L_c,$$

where g is the total length on hardpart radius function, L_i is back-calculated TL at age i, S_i is the measured hardpart size at annulus i, and S_c and L_c are the respective hardpart size and total length at capture. Only fish collected in April and May—the beginning of the somatic growth season—were used, to remove seasonal effects from the back-calculation equations (Ricker, 1992). Because body-proportional back-calculation is based not just on the relationship of hardpart size to total length but also on the relationship of hardpart size to consecutive annuli, mean annual growth increments were also calculated and compared between scales and otoliths.

The tendency for older fish to produce smaller back-calculated lengths at younger ages than observed, known as Lee's phenomenon (Smith, 1983), was evaluated by calculating mean SAR and mean OAR for each age at capture. In this way it was possible to determine if older fish demonstrated slower hardpart growth at younger ages, i.e. true Lee's phenomenon (Smale and Taylor, 1987).

Data were analyzed by using χ^2 tests and regression methods available through the Statistical Analysis System (SAS 1988). Rejection of the null hypothesis in statistical tests was based on α=0.05. Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981).

Results

Preliminary comparison of hardparts

All four hardparts showed concentric marks that were interpreted as annuli (Fig. 2). However, marks on the dorsal spines and pectoral rays were inconsistent, often blurred or impossible to follow around most of the section and therefore difficult to interpret. Presumed annuli on scales were distinctly clearer and more regular than those on dorsal spines and pectoral rays, but they still required some subjective interpretation. Presumed annuli on otoliths were exceptionally clear, consistent, and easy to interpret.

Typical otolith sections showed an opaque nucleus surrounded by a translucent zone followed by a pattern of thin, opaque zones alternating with wide, translucent zones along the sulcal groove (Fig. 2A). In some sections the translucent zone between the nucleus and the first opaque zone was relatively small and made more opaque by a number of fine, circular, opaque bands. However, in all sections the first opaque zone beyond the nucleus was easily identified and considered to be the first annulus.

Presumed annuli on scales were harder to identify than those on otoliths but were usually identifiable as a clear zone in the anterior field, where circuli are either absent or more widely spaced, and by cutting over in the lateral fields (Fig. 2D). Checks were most apparent in the anterior field. A clear zone in the anterior field was considered a check if it was not accompanied by distinct cutting over in the lateral fields. The first annulus was the hardest to identify. It rarely showed a clear band in the radii zone, although cutting over was sometimes apparent. Its position was based predominantly on the first point at which a large number of secondary radii originated.

Presumed annual marks on dorsal spines were fairly clear in some sections but incomplete or blurred in others (Fig. 2C), whereas pectoral-fin ray sections were consistently hard to interpret (Fig. 2B). Presumed annual marks on both these hardparts appeared as wide, opaque, semicircular bands alternating with narrow translucent zones.

Otoliths showed the greatest precision, with 100% average agreement within and between readers. Scales also had high average agreement: 89% within readers and 80% between readers. Dorsal and pectoral fin sections showed the lowest agreement (Table 1) and little confidence was attached to their age assignments.

Table 1

Average percent agreement in the preliminary comparison of weakfish, *Cynscion regalis*, hardpart mark counts within readers, between readers, and with otoliths.

Hardpart	Within readers	Between readers	With otoliths
Scales	89	80	27
Pectoral rays	59	64	49
Dorsal spines	66	76	46
Otoliths	100	100	

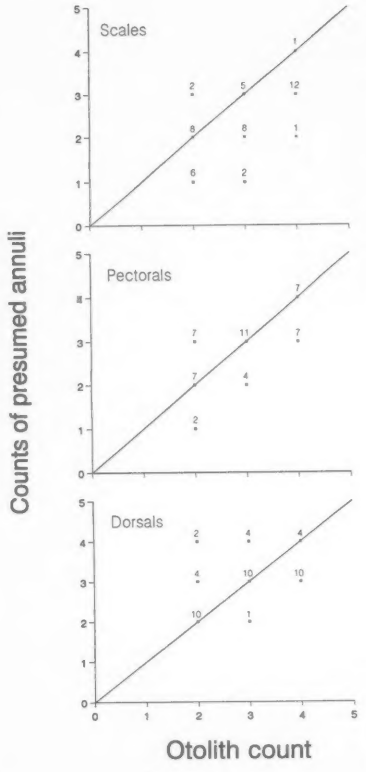


Figure 3

Counts of presumed annuli from weakfish, *Cynoscion regalis*, scales, pectorals, and dorsals compared with otoliths. The number of fish each point represents is indicated. The 45° line represents 100% agreement.

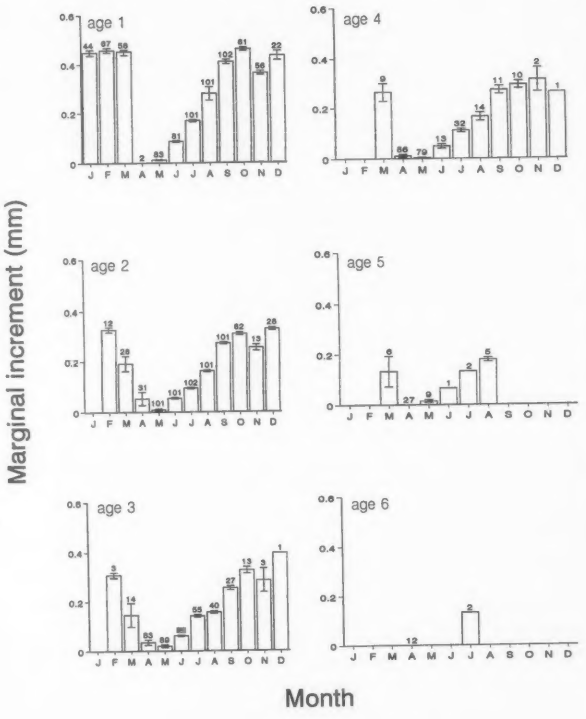


Figure 4

Mean monthly otolith marginal increments for weakfish, *Cynoscion regalis*, ages 1–6 from the Chesapeake Bay region, 1989–91. Vertical bars are ± one standard error. Numbers above the bars represent sample size.

The number of presumed annual marks on otolith sections agreed poorly with those on other hardparts (Fig. 3). Scale and otolith readings agreed only 27% of the time (Table 1) and scales consistently had one less mark than otoliths (26 out of 45). Pectoral and dorsal rays showed better agreement with otoliths than with scales, 49% and 46% respectively.

Validation of the otolith method

Opaque bands are laid down on otoliths once a year in the spring. Mean monthly marginal increment plots for ages 1–6 showed only one trough during the year, indicating only one opaque band was formed per year (Fig. 4). A few fish began to lay down annuli in March, as shown by the decrease in mean marginal increment and a relatively high variation in marginal increment size. However, lowest marginal increment values occurred in April and May, indicating most fish formed annuli during these months. Greatest otolith growth occurred during the months of June, July, August, and September, as demonstrated by the step-wise increase in mean marginal increments. By October, mean marginal increments reached a fairly stable maximum, indicating little or no otolith growth. This maximum continued until the next March or April, when annuli were again laid down.

Because of the scarcity of older fish, it was not possible to validate conclusively fish older than age 5 by separate marginal increment plots. However, there was no evidence that the pattern of annulus formation changed within the weakfish lifespan. Annuli were consistently formed during March–May for fish of different sizes, sexes, and ages (1–6), and otoliths did not form more than one mark per year even though these ages represented various stages in the

fish's life history. Additionally, of the 2,217 otoliths examined (ages 1–10), all those in the process of forming or which had just formed annuli were collected in March–May. Thus, we assumed for ages 1–10 that the otolith method provided accurate ages.

Comparison of scales and otoliths

Scales were consistently more difficult to read than otoliths, and confidence in scale readings was often low. Percent agreement within and between readers was fairly consistent for both hardparts. However, otoliths showed much higher agreement (98–100%), than did scales (78–80%) (Table 2). Although agreement between scales and otoliths was fairly high, 79%, agreement decreased with increasing age. Of 32 disagreements, only 6 differed by more than one year (Fig. 5). However, 4 of the 5 fish older than age 6 were underaged by scales and two of the oldest fish, age 10 and 8, were underaged by 3 years. Scales from older fish, if they showed more than 6 annuli, had marks which were severely crowded and fragmented even when viewed at higher magnification (Fig. 6A), whereas otoliths from these same fish showed clear annuli (Fig. 6B).

Although the number of fish underaged was small, their effect on estimating growth curves would be dramatic. Mean body size at age based on scales, although slightly curvilinear, showed no clear indication of an asymptote (Fig. 7A) and thus would not be appropriate for fitting a von Bertalanffy growth curve (Gallucci and Quinn, 1979). In contrast, mean body size at age based on otoliths showed the clear beginnings of an asymptote (Fig. 7B).

Although sex of the fish had no effect on the precision or repeatability of scale readings, it did affect accuracy. Agreement of scale ages among and between readers was quite similar when calculated separately by sex, ranging from 75 to 79.5%. However, agreement between scale and otolith ages, or accuracy, was significantly different for males and females (χ^2=6.25, n=154, P<0.05). Of the 32 discrepancies between scale and otolith ages, 26 of them were males. Even if the fish greater than age 6 are discounted, there is still a significant difference (χ^2=5.79, n=149, P<0.05).

Time of annulus formation is not the same for scales and otoliths. Both hardparts showed only one trough in their mean monthly marginal increments (Fig. 8). However, otoliths with annuli on their margins were collected only during a discrete time period, 1 April–1 June, while scales in the process of forming annuli were collected from mid-April to mid-August, although most scales formed annuli in August. The variable and extended time of scale annulus formation is represented by the shallow trough (Brothers, 1983) and the larger standard errors of the scale marginal increment plot, as compared with that of otoliths (Fig. 8).

Although total length on hardpart size relationships for both scales and otoliths showed linear trends (r^2=0.94 and 0.88 respectively, n=175, P=0.0001), the total length on otolith relationship showed seasonal variation. When a single age class (age 3) was marked by season of collection and plotted against the linear relationship predicted by the total sample (Fig. 9), all fish collected in April and May had smaller than predicted otolith radii, whereas fish collected in August and September had larger than predicted radii. Fish collected in June and July were intermediate, although most of their radii were also smaller than predicted. Scales from the same fish did not show similar seasonal trends.

Back-calculation equations of total length on hardpart size were calculated only for fish collected at the beginning of the growing season, in April and

Table 2

Percent agreement of weakfish, *Cynoscion regalis*, scale- and otolith-assigned ages within readers, between readers, and between hardparts.

Hardpart	Within reader 1	Within reader 2	Between readers	With otoliths
Scales	80	78	80	79
Otoliths	100	98	99	

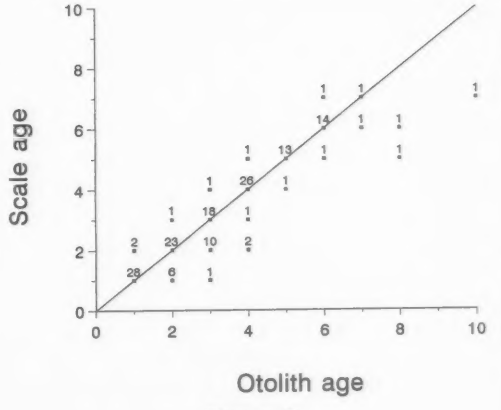


Figure 5

Weakfish, *Cynoscion regalis*, assigned ages from scales and otoliths. The number of fish each point represents is indicated. The 45° line represents 100% agreement.

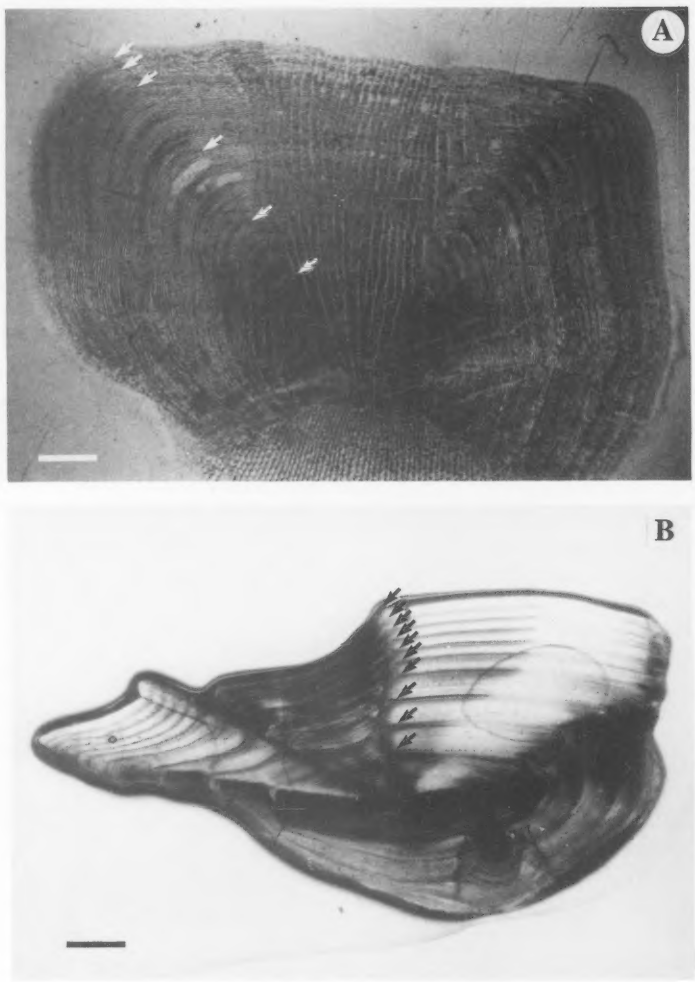


Figure 6

The scale impression (**A**) and sectioned otolith (**B**), as seen in transmitted light, from a male, 10-year-old weakfish, *Cynoscion regalis*, TL=845 mm, collected in mid-May. Arrows indicate marks counted as annuli.

May, to remove seasonal effects. Although linear regressions were significant for scales (r^2=0.95, P=0.0001) and otoliths (r^2=0.92, P=0.0001), a quadratic term improved the model fit and was significant (P=0.0003 scales, P=0.0001 otoliths) (Fig. 10). Equations were

For scales:

$$TL = -151.6 + 160.2\ SR - 5.4\ SR^2\ (r^2=0.96, n=88, P=0.0001);$$

For otoliths:

$$TL = -220.9 + 543.1\ OR - 66.9\ OR^2\ (r^2=0.94, n=88, P=0.0001).$$

The pattern of mean annual growth increments differed between scales and otoliths. Both scales and otoliths showed their largest growth increment from the focus to the first annulus (Fig. 11). However, once fish had reached age 1, the largest otolith annual growth increment occurred between the first and

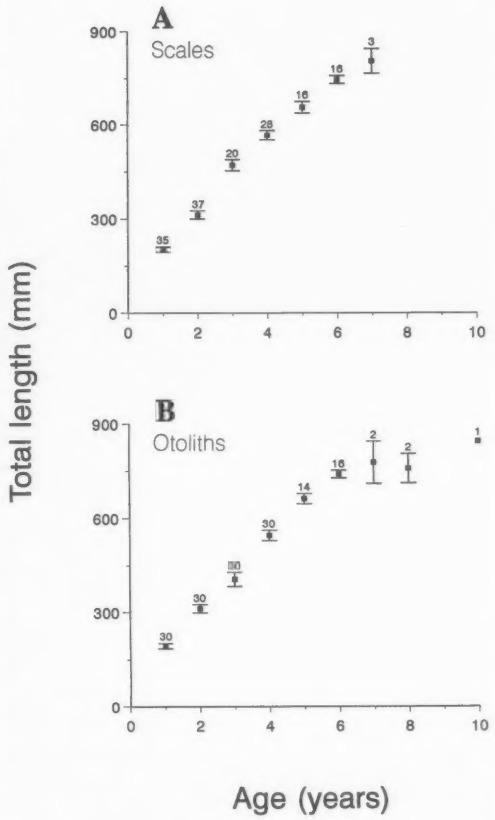


Figure 7

Mean weakfish, *Cynoscion regalis*, size at age: (**A**) based on scales and (**B**) based on otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample size.

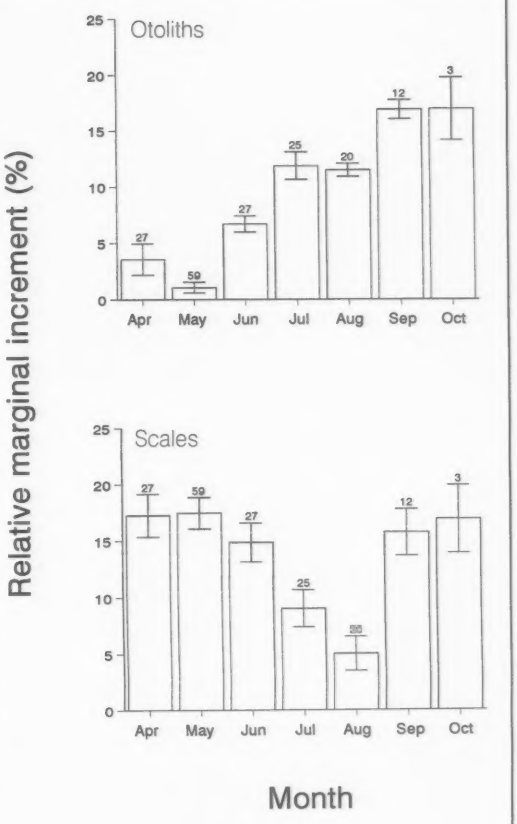


Figure 8

Mean monthly relative increments for weakfish, *Cynoscion regalis*, scales and otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample sizes.

second annuli, whereas scales had a very small increment between these annuli. The largest scale growth increment after age 1 was between annuli 3 and 4. Neither hardpart showed a consistently decreasing mean annual growth increment as age increased. Although this assumption is often included in scale-reading criteria, it would be inappropriate for weakfish.

Back-calculated mean body sizes at age were larger for scales than for otoliths (Table 3). In part, this discrepancy may reflect different times of annulus formation: back-calculated lengths from scales, in general, estimate sizes in August, whereas back-calculated lengths from otoliths estimate sizes in April and May. Also, at older ages, back-calculated body sizes at age based on scales would be expected to be larger because of the underageing of older fish by scales.

Both scales and otoliths showed smaller back-calculated mean body size at age 1 than observed. At later ages, back-calculated TL's from scales were larger than observed, while back-calculated TL's from otoliths showed no consistent trend (Table 3). The cause of the smaller back-calculated TL's at age 1, however, did not appear related to Lee's phenomenon, as there was no consistent trend of smaller age-1 annular radii at older ages at capture (Tables 4 and 5). In fact, the largest mean SAR and OAR at age 1 came from 5-year-old fish. However, age-1 OAR's from the oldest fish in the study (>age 6, n=5) were distinctly smaller than those observed in younger fish.

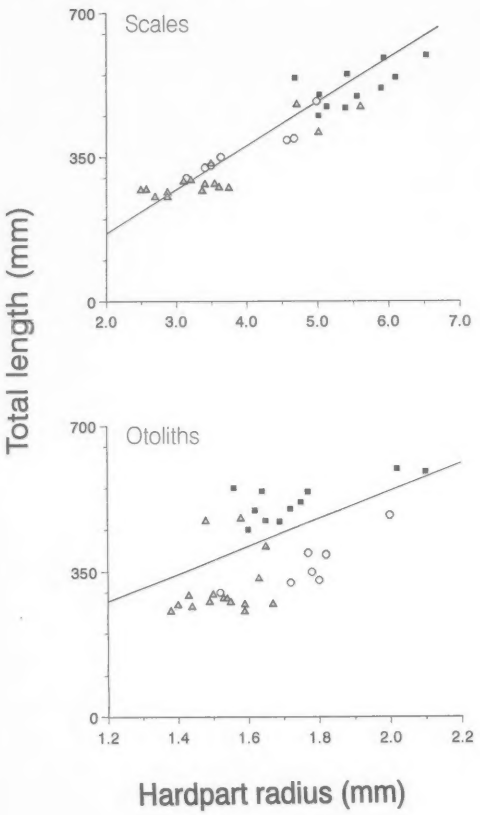


Figure 9

Total length plotted on hardpart size for age-3 weakfish, *Cynoscion regalis*, n=35. Lines represent the linear total length to hardpart regressions calculated from all fish, n=175. Fish are marked by season of collection: open circles=April–May; shaded triangles=June–July; and black squares=August–September.

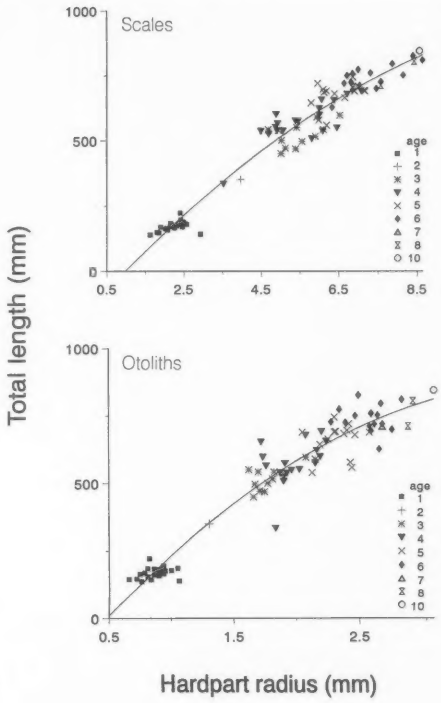


Figure 10

Weakfish, *Cynoscion regalis*, total length on hardpart radius regression used for back calculation. Based on fish collected in April and May, n=88.

Discussion

Our results indicate that transverse otolith sections are the best method to age weakfish. Sectioned otoliths were characterized by thin opaque bands, considered annuli, interspersed with wider translucent zones. This pattern is similar to other sciaenids, such as spotted seatrout, *Cynoscion nebulosus* (Maceina et al., 1987), Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994), red drum, *Sciaenops ocellatus* (Murphy and Taylor, 1991), and black drum, *Pogonias cromis* (Beckman et al., 1990). This pattern should not be confused with the more

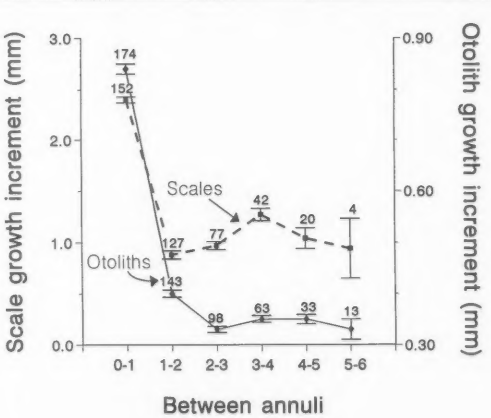


Figure 11

Mean annual growth increments of weakfish, *Cynoscion regalis*, scales and otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample sizes.

common otolith pattern found in many temperate fish of thin translucent zones, which are considered annuli, interspersed with wide opaque zones (Hyndes et al., 1992).

Table 3

Mean back-calculated weakfish, *Cynoscion regalis*, total lengths (mm) at age based on scales and otoliths, calculated from a quadratic body to hardpart regression and observed mean total length at time of annulus formation. Sample size is in parentheses.

Age	Scales	Observed Jul/Aug	Otoliths	Observed April/May
1	196 (152)	240 (7)	162 (174)	172 (22)
2	305 (127)	296 (25)	297 (144)	260 (2)
3	422 (77)	377 (8)	421 (99)	532 (12)
4	564 (42)	514 (5)	552 (64)	566 (18)
5	682 (20)		660 (34)	663 (14)
6	733 (4)		711 (14)	741 (16)
7			750 (5)	710 (1)
8			748 (2)	759 (2)
10				845 (1)

Table 4

Mean scale annular radii (SAR) for each scale age of weakfish, *Cynoscion regalis*.

		Scale annulus					
Age	*n*	1	2	3	4	5	6
1	12	2.59					
2	52	2.31	3.20				
3	24	2.40	3.42	4.14			
4	29	2.38	3.27	4.27	5.56		
5	16	2.65	3.44	4.31	5.43	7.15	
6	16	2.38	3.25	4.30	5.58	6.64	7.00
7	3	2.11	3.09	3.92	5.65	6.69	7.37

Table 5

Mean otolith annular radii (OAR) for each otolith age of weakfish, *Cynoscion regalis*.

		Otolith annulus							
Age	*n*	1	2	3	4	5	6	7	8
1	29	0.83							
2	45	0.85	1.27						
3	35	0.82	1.21	1.56					
4	30	0.82	1.20	1.53	1.91				
5	14	0.88	1.25	1.58	1.91	2.28			
6	16	0.86	1.22	1.54	1.88	2.21	2.52		
7	2	0.80	1.18	1.47	1.79	2.16	2.47	2.79	
8	2	0.77	1.20	1.56	1.90	2.22	2.47	2.65	2.85
10	1	0.67	1.11	1.52	1.94	2.15	2.32	2.49	2.67

Sectioned otoliths were consistently clear and easy to read, as shown by the high precision of repeated age readings. Although it was possible only to validate ages 1–5 by separate marginal increment plots, otolith annuli in all ages examined (1–10) were laid down once a year during a discrete time period (April–May). The constancy of annulus deposition at older ages, the lack of severely crowded annuli in older fish, and the similarity between weakfish otoliths and other sciaenid otoliths that have been validated at older ages (Beckman et al., 1990, Murphy and Taylor, 1991; Barbieri et al., 1994) suggest that otoliths are a reliable ageing technique for weakfish, although older ages must still be validated.

In contrast, we found the scale method of ageing weakfish to be imprecise and apparently inaccurate at older ages. We found that scales form annuli over an extended period, April–August, similar to the results of past studies (Perlmutter et al., 1956; Massmann, 1963b). This protracted period of annulus formation made it difficult to assign ages to fish taken in midsummer with moderate growth on the scale margin, as noted by Massmann (1963b). For example, a fish taken in July with a medium marginal increment on its scale could have formed its annuli in early April and have grown since then, or it could have increased its growth increment before forming an annulus in August. Thus, assigning an age to these fish is purely subjective and can lead to ageing errors ± one year, which may explain most of the discrepancies between otolith and scale ages.

The long period of annulus formation on scales and the severe crowding of annuli at older ages make it difficult to validate scales by the marginal increment method—as Perlmutter et al. (1956) and Shepherd and Grimes (1983) attempted for pooled age data. Because scale annuli form over a protracted period, the trough in the marginal increment plot is shallow and the range of marginal growth during other months is large. Additionally, validation by the marginal increment method is not appropriate if the hardpart shows severe crowding of annuli at older ages, as we found with scales, and has been previously reported (Shepherd, 1988). Shepherd (1988) described annuli in fish older than age 6 or 7 as being crowded and very difficult to detect, which could lead to marginal increments being measured from the last distinguishable annulus to the edge, rather than from the last real annulus to the edge. This error would inflate marginal increment estimates and there would be no way to detect underaged, older fish in marginal increment plots.

The scale method appears to underage older weakfish. Assuming otolith ages were valid, 4 of the 5 fish in this study older than age 6 were underaged by scales. Although 4 out of 155 fish may seem insignificant, the importance of correctly ageing these fish cannot be judged only by the number of discrepancies. These fish represent the beginning of an asymptote in growth and fish in the asymptotic range are often rare in highly exploited stocks. Obtaining and correctly ageing a few weakfish in this range is critical to correctly estimating the parameters of the von Bertalanffy growth curve.

Annulus formation on weakfish otoliths and scales shows different patterns. The formation of otolith annuli over a discrete time period suggests it may be caused by environmental variables. The most commonly suggested environmental influences on annulus formation are temperature, salinity, food, and light (Simkiss, 1974). Weakfish form annuli on their otoliths in April and May, when they migrate from offshore winter grounds to estuarine feeding and spawning grounds. Thus, annulus formation may be linked to their migration into a different environment.

Weakfish scales, in contrast, have a more variable time of annulus formation suggesting a cause other than general environmental conditions. Scales may undergo resorption whereas otoliths do not (Simkiss, 1974), and spawning has been linked to scale resorption with a consequent scale mark in salmon and trout (Crichton, 1935). Spawning may also be linked to formation of annuli on weakfish scales (Merriner, 1973). Weakfish mature at age 1 (Merriner, 1976; Shepherd and Grimes, 1984) and are multiple spawners with a protracted spawning period from May through August (Lowerre-Barbieri[2]). However, individual spawning periods are asynchronous and vary greatly, especially in time of termination. Spawning activity and annulus formation may be linked in two ways: 1) annuli could form on scales early in the spawning season when resources are shifted towards production of reproductive materials—especially the yolking of oocytes, or 2) annuli might form near the end of the season, owing to the cumulative drain of protracted spawning, causing a cessation in growth and thus an annulus. A connection between scale annulus formation and spawning in weakfish would explain the high level of variation in time of annulus formation and the higher accuracy of ages based on scales taken from females, because females usually invest more energy in reproduction. It might also explain the small growth increment between annuli 1 and 2 if one-year-old weakfish begin spawning later in the season than older fish, owing to a threshold size necessary to reach maturity.

Our results indicate both scales and otoliths present problems for back-calculation of weakfish. Although scales showed a strong relationship between body and hardpart size and no seasonal differences in growth, their long and variable time of annulus formation may cause considerable error (Smith, 1983). It is impossible to determine if a fish formed its annuli at the same time each year. Because annuli can form from April to August, increments may represent 8–16 months of growth rather than approximately one year of growth. Additionally, scale annuli are more difficult to distinguish than otolith annuli, making SAR's difficult to measure and somewhat subjective. However, otoliths show seasonal change in the body to hardpart relationship, making a season-specific back-calculation equation, such as we developed, inappropriate for fish collected outside of that season. Additionally, comparisons between back-calculated and observed sizes at age were complicated by the weakfish migrational pattern, since weakfish age ranges in the Chesapeake Bay vary seasonally—older fish are present only in spring and only occasionally in fall (Joseph, 1972).

There was no clear evidence of Lee's phenomenon, as older fish did not consistently show smaller hardpart size at younger ages. The five oldest fish did, however, demonstrate considerably smaller OAR's at age 1 than did their younger counterparts. Nevertheless, these same fish did not demonstrate consistently smaller OAR's at consecutive ages than did younger fish. Thus, the smaller OAR's at age 1, rather than demonstrating Lee's phenomenon, may simply reflect when most fish of those year classes were born, i.e. fish born early in the spawning season would have larger OAR's at age 1 because they had more time to grow before winter, than did fish born later in the season.

Previous criticism of back-calculation has focused mainly on the body size to hardpart relationship and its calculation (Campana, 1990; Casselman, 1990; Francis, 1990; Ricker, 1992). However, the validity of back-calculation also depends on the constancy, clarity, and pattern of hardpart growth increments. The different growth increment patterns we found between scales and otoliths demonstrate the need to understand hardpart growth better, how it relates to somatic growth and what causes annulus formation on different hardparts.

Future studies of weakfish age and growth should be based on sectioned otoliths because scales appear inaccurate once growth becomes asymptotic. This common failing of the scale method has been reported for many species (Beamish and McFarlane, 1987). It

[2] Lowerre-Barbieri, S. K. 1993. Reproductive biology of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region. School of Marine Science, VIMS, College of William and Mary, unpubl. manuscr.

can result in underestimates of longevity, overestimates of mortality, inaccurate growth calculations, and improper modelling and management decisions (Beamish and McFarlane, 1983). Similarly, current estimates of weakfish growth, longevity, and mortality may need to be reevaluated, as suggested by our findings that scales underage older fish and have crowded annuli past age 6. The need for this reevaluation is underscored by the recording of a 17-year-old, as aged by otoliths, which was previously aged as a 7-year-old by scales (Lowerre-Barbieri[3]).

Acknowledgments

We would like to thank the Chesapeake Bay commercial fishermen, James Owens, and the people at the Delaware Weakfish Sport Fishing Tournament for helping us obtain samples. Richard Seagraves provided us with information on the Delaware fishery as well as otolith samples. Steve Bobko and Donna Kline helped with the processing and original analysis of the four hardparts. We would like to thank J. M. Casselman, Luiz R. R. Barbieri, and an anonymous reviewer for their helpful suggestions to improve the manuscript. Financial support was provided by the College of William and Mary, Virginia Institute of Marine Science, by Old Dominion University, Applied Marine Research Laboratory, and by a Wallop/Breaux Program Grant from the U.S. Fish and Wildlife Service through the Virginia Marine Resources Commission for Sport Fish Restoration, Project No. F–88-R3.

Literature cited

Bagenal, T. B., and F. W. Tesch.
1978. Age and growth. *In* T. B. Bagenal (ed.), Methods for assessment of fish production in fresh waters, 3rd ed., p. 101–136. Blackwell Scientific Publs., Oxford.

Barbieri, L. R., M. E. Chittenden Jr., and C. M. Jones.
1994. Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region, with a discussion of apparent geographic changes in population dynamics. Fish. Bull. 92:1–12.

Barnes, M. A., and G. Power.
1984. A comparison of otolith and scale ages for western Labrador lake whitefish (*Coregonus clupeaformis*). Env. Biol. Fish. 10:297–299.

Beamish, R. J.
1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can. 36:141–151.

Beamish, R. J., and D. E. Chilton.
1981. Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). Can. J. Fish. Aquat. Sci. 39:277–287.

Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.
1987. Current trends in age determination methodology. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 15–42. Iowa State Univ. Press, Ames.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson.
1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish Bull. 53:1–577.

Brothers, E. B.
1983. Summary of round table discussions on age validation. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:35–44.

Campana, S. E.
1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47:2219–2227.

Casselman, J. M.
1983. Age and growth assessment of fish from their calcified structures—techniques and tools. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:1–17.
1987. Determination of age and growth. *In* A. H. Weatherley and H. S. Gill (eds.), The biology of fish growth, p. 209–242. Academic Press, London.
1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119:673–688.

Crichton, M. I.
1935. Scale resorption in salmon and sea trout. Salm. Fish., Edinb. 4:1–8.

Draper, N. R., and H. Smith.
1981. Applied regression analysis, 2nd ed. John Wiley & Sons, New York, 709 p.

Francis, R. I. C. C.
1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36:883–902.

Gallucci, V. F., and T. J. Quinn II.
1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14–25.

Hyndes, G. A., N. R. Loneragan, and I. C. Potter.
1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead, *Platycephalus speculator*. Fish. Bull. 90:276–284.

Joseph, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87–100.

[3] Lowerre-Barbieri, S. K. 1993. Age and growth of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region. School of Marine Science, VIMS, College of William and Mary, unpubl. manuscr.

Maceina, M. J., D. N. Hata, T. L. Linton, and A. M. Landry Jr.
1987. Age and growth analysis of spotted seatrout from Galveston Bay, Texas. Trans. Am. Fish. Soc. 116:54–59.

Massmann, W. H.
1963a. Age and size composition of weakfish, *Cynoscion regalis*, from pound nets in Chesapeake Bay, Virginia, 1954–1958. Chesapeake Sci. 4:43–51.
1963b. Annulus formation on the scales of weakfish, *Cynoscion regalis*, of Chesapeake Bay. Chesapeake Sci. 4:54–56.

Massmann, W. H., J. P. Whitcomb, and A. L. Pacheco.
1958. Distribution and abundance of gray weakfish in the York River system, Virginia. Trans. N. Am. Wildl. Conf. 23:361–369.

Mercer, L. P.
1985. Fishery management plan for the weakfish (*Cynoscion regalis*) fishery. North Carolina Dep. Nat. Res. Comm. Dev., Div. Mar. Fish., Spec. Sci. Rep. 46, 129 p.

Merriner, J. V.
1973. Assessment of the weakfish resource, a suggested management plan, and aspects of life history in North Carolina. Ph.D. diss., North Carolina State Univ., Raleigh, NC, 201 p.
1976. Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina. Fish Bull. 74:18–26.

Murphy, M. D., and R. G. Taylor.
1991. Direct validation of ages determined for adult red drums from otolith sections. Trans. Am. Fish. Soc. 120:267–269.

Nesbit, R. A.
1954. Weakfish migration in relation to its conservation. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 115, 81 p.

Pearson, J. C.
1932. Winter trawl fishery off the Virginia and North Carolina coasts. U.S. Bur. Fish. Invest. Rep. 10, 31 p.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout *Cynoscion regalis* (Bloch and Schneider). U.S. Fish Wildl. Serv. Fish Bull. 50:79–102.

Perlmutter, A., W. S. Miller, and J. C. Poole.
1956. The weakfish (*Cynoscion regalis*) in New York waters. N.Y. Fish Game J. 3:1–43.

Ricker, W. E.
1992. Back-calculation of fish lengths based on proportionality between scale and length increments. Can. J. Fish. Aquat. Sci. 49:1018–1026.

Rothschild, B. J., P. W. Jones, and J. S. Wilson.
1981. Trends in Chesapeake Bay fisheries. Trans. N. Am. Wildl. Conf. 46:284–298.

SAS.
1988. SAS/STAT User's Guide, Release 6.03 ed. SAS Institute Inc., Cary, NC, 1029 p.

Shepherd, G. R.
1988. Age determination methods for northwest Atlantic species, weakfish *Cynoscion regalis*. *In* J. Penttila and L. M. Derry (eds.), Age determination methods for northwest Atlantic species, p.71–76. NOAA Tech. Rep. NMFS 72, 135 p.

Shepherd, G. R., and C. B. Grimes.
1983. Geographic and historic variations in growth of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight. Fish. Bull. 81:803–813.
1984. Reproduction of weakfish, *Cynoscion regalis*, in the New York bight and evidence for geographically specific life history characteristics. Fish. Bull. 82:501–511.

Simkiss, K.
1974. Calcium metabolism of fish in relation to ageing. *In* T. B. Bagenal (ed), The ageing of fish, p. 1–12. The Gresham Press, Old Woking, Surrey, England.

Smale, M. A., and W. W. Taylor.
1987. Sources of back-calculation error in estimating growth of lake whitefish. *In* R. C. Summerfelt and G.E. Hall (eds.), Age and growth of fish, p. 189–202. Iowa State Univ. Press, Ames.

Smith, C. L.
1983. Summary of round table discussions on back calculation. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:45–47.

Taylor, H. F.
1916. The structure and growth of the scales of the squeteague and the pigfish as indicative of life history. Bull. U.S. Bur. Fish. 34:285–330.

Villoso, E. P.
1989. Reproductive biology and environmental control of spawning cycle of weakfish, *Cynoscion regalis* (Bloch and Schneider), in Delaware Bay. Ph.D. diss., Univ. Delaware, Newark, 295 p.

Welsh, W. W., and C. M. Breder Jr.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141–201.

Whitney, R. R., and K. D. Carlander
1956. Interpretation of body-scale regression for computing body length of fish. J. Wildl. Mgmt. 20(1):21–27.

Wilk, S. J.
1979. Biological and fisheries data on weakfish, *Cynoscion regalis* (Bloch and Schneider). U.S. Dep. Commer., NOAA, NMFS, NEFC, Sandy Hook Laboratory, Tech. Ser. Rep. No. 21, 49 p.

Williams, T., and B. C. Bedford.
1974. The use of otoliths for age determination. *In* T. B. Bagenal (ed), The ageing of fish, p. 114–123. The Gresham Press, Old Woking, Surrey, England.

Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of central Peru

Jeff McKinnon

Department of Zoology, The University of Guelph
Guelph, Ontario, Canada N1G 2W1
Present address: The Biological Laboratories, Harvard University
16 Divinity Ave, Cambridge, MA 02138

Abstract.—In this study of the feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, stomach content samples were collected from dolphins caught by an artisanal fishery operating along the central coast of Peru. Collections were made from three fishing ports, Pucusana, Ancon, and Cerro Azul, during the summers and winters of 1985 and 1986. Overall, the anchoveta, *Engraulis ringens*, the most abundant vertebrate in Peruvian coastal waters, was the principal prey of dusky dolphins with respect to each of four different measures of dietary importance. Anchoveta was also the dominant prey in both seasons of both years, and for all reproductive classes of dusky dolphins. Other prey species commonly found in dolphin stomachs were horse mackerel, *Trachurus symmetricus*, hake, *Merluccius gayi*, sardine, *Sardinops sagax*, Patagonian squid, *Loligo gahi*, and jumbo flying squid, *Dosidicas gigas*. Regressions of body size on otolith or squid beak dimensions were used to estimate lengths and weights of anchoveta and some other prey. All prey species averaged less than 30 cm in estimated length and 300 g in weight. Estimated total lengths of anchoveta consumed as prey increased between seasons in 1985 and between years, paralleling the lengths of anchoveta taken by the purse-seine fishery. However, estimated total lengths of anchoveta eaten by dusky dolphins were consistently smaller than lengths of those caught by the fishery.

Manuscript accepted 11 November 1993.
Fishery Bulletin 92:569–578 (1994).

The dusky dolphin, *Lagenorhynchus obscurus*, is common in the coastal waters of New Zealand, South America, and South Africa, but like most species of small cetacea from the Southern Hemisphere, its feeding habits are poorly described (Gaskin, 1982; Goodall and Galeazzi, 1985). The squid, *Nototodarus sloanei*, and fish have been reported as prey in New Zealand waters (Gaskin, 1972), whereas in Argentina Würsig and Würsig (1980) observed dusky dolphins feeding on southern anchovy, *Engraulis anchoita*. Prior to the present study, little was known of the feeding habits or natural history of the dusky dolphin in Peruvian waters, although large numbers of dusky dolphins were being taken in an artisanal fishery (Read et al., 1988; Van Waerebeek and Reyes, 1990).

In Peru, the dusky dolphin is found in the waters of the coastal upwelling system (McKinnon, 1988), which has been extensively studied by those involved in managing the system's various fisheries (Pauly and Tsukayama, 1987; Pauly et al., 1989). The cool waters of the coastal upwelling region constitute one of the most productive areas of the world ocean (Ryther, 1969), but oceanographic conditions and the abundance and distribution of fishes can vary greatly within and between years, especially when El Niño's occur (Pauly and Tsukayama, 1987; Pauly et al., 1989).

The objective of the present study was to characterize, in terms of both species composition and prey size, the feeding habits of the dusky dolphin in Peruvian waters. Seasonal and annual variation in feeding habits was also investigated and compared with abundance data for important prey species during the same periods. In addition, potential dietary differences among dolphins of different reproductive states were examined, as feeding habits of lactating females differ from those of nonlactating females and males in some small cetaceans (Bernard and Hohn, 1989; Recchia and Read, 1989).

Methods

Data on feeding habits were obtained by analysis of undigested hard parts of prey, specifically fish otoliths and squid beaks, from stomach content samples collected through the fishery. Dolphins were usually captured by artisanal fishermen in gill nets set from dusk to dawn within the coastal upwelling zone (Read et al., 1988; Van Waerebeek and Reyes, 1990), but six stomach samples from a single landing by a purse seiner, in the summer of 1985, were also included.

All samples were collected at ports along the central coast of Peru, where the largest dolphin catches occurred during the present

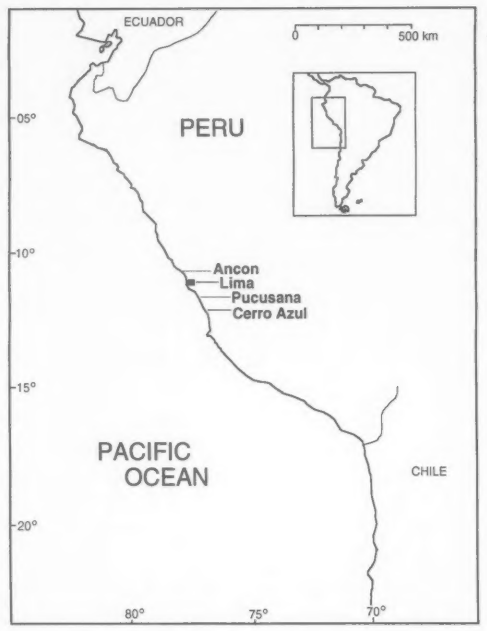


Figure 1

Map of Peruvian coastline, showing study sites. The inset shows the area in relation to the remainder of South America (Read et al., 1988).

study (Read et al., 1988). Pucusana, a small fishing town approximately 50 km south of Lima (Fig. 1) was the principal collecting site. Stomach content samples were also collected from the nearby ports of Cerro Azul and Ancon, about 70 km south and 90 km north of Pucusana, respectively (Fig. 1). Dolphin landings at any given port were highly variable (Read et al., 1988), therefore collecting efforts were concentrated at the port or ports where the most dolphins were being caught. The collecting periods were the austral summers (1 January through 31 March) and winters (1 July through 30 September) of 1985 and 1986.

Field procedures

Standard length, measured in a straight line along the main axis of the body from the tip of the upper jaw to the notch of the flukes, was taken for each specimen upon being landed. Females were pressed above the nipples and expression of milk, indicating lactation, was noted. When dolphins were eviscerated, female reproductive tracts were removed and checked for the presence of a fetus. Ovaries were inspected for corpora lutea and albicantia, then preserved in 10% formalin.

Collection of stomach contents also began upon evisceration, between approximately 6 and 48 hours after capture. Each of the fore-, main, and pyloric stomachs was separately rinsed through a series of three brass sieves (Treacy and Crawford, 1981; Murie and Lavigne, 1985) of mesh diameters 4.75, 1.40, and 0.425 mm. The sieved contents were then placed in deep, water-filled plastic trays so that any remaining flesh could be skimmed off. Fish otoliths and clean squid beaks were retrieved and stored in 5–10% alcohol; squid beaks with flesh still attached were stored in either 70% alcohol or 10% formalin. The forestomach consistently contained the least digested contents and the greatest volume, so only material from that chamber was later quantified and analyzed (see also Perrin et al., 1973; Bernard and Hohn, 1989).

Reproductive status

Reproductive status of females was classified after macroscopic examination of gonads and accessory reproductive tissues. Males were classified only as to sex. Females were defined as 1) immature, if their ovaries lacked corpora lutea and albicantia; 2) pregnant, if a fetus was visible in the uterus; 3) lactating; 4) simultaneously pregnant and lactating; or 5) resting, if corpora lutea or albicantia were present but there was neither a fetus visible in the uterus nor evidence of lactation (Perrin and Donovan, 1984). The "resting" category may have included females with small embryos not detected during field inspections, in addition to individuals actually between reproductive cycles (Perrin and Donovan, 1984). Data were incomplete for several females; therefore they were classified as "unknown females." No information on gender was available for several additional samples; their sex and reproductive status were classified as "unknown."

Identification of prey and calculation of measures of relative importance

A reference collection of otoliths from common Peruvian marine fishes was made from specimens purchased at local markets and identified with Chirichigno's (1978) key. Otoliths from stomach contents were identified by comparison with this collection and collections belonging to the Instituto del Mar del Peru (IMARPE) and to P. Majluf (University of Cambridge). Squid species were identified from their beaks by using published keys (Wolff, 1984; Clarke, 1986), through reference to beaks from local squids identified and supplied by F. Cardoso (Museo de

Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), and with the assistance of S. Candela (University of Miami, Florida).

Counts and measurements of undigested hard parts of prey allowed calculation of several measures of the relative importance of each prey species. The simplest measure, "percent frequency of occurrence", was defined as 100 multiplied by the number of stomachs in which a prey species was present/the total number of stomachs in the sample, excluding empty stomachs. "Percent total numbers," was defined as 100 multiplied by the number of individuals of a species of prey/the sum of individuals for all prey species (Frost and Lowry, 1980). The number of individuals of each prey species in a sample was estimated by dividing the count of its otoliths (for fish) or squid beaks (for squid) by two (Frost and Lowry, 1980).

Lengths and weights of consumed fish were estimated by using regressions involving fish length and otolith length, or fish weight and either fish length or otolith length. Calculations for anchoveta, *Engraulis ringens*, Pacific Sardine, *Sardinops sagax*, hake, *Merluccius gayi*, and horse mackerel, *Trachurus symmetricus*, followed Chirinos and Chuman (1968), Samame (1977), McKinnon (1988), and Hawes (1983), respectively, except that length was estimated for *T. symmetricus* by using $L=4.37\times W^{1/3}$, and weights of *E. ringens* and *S. sagax* were estimated by using $W=0.007\times L^3$ and $W=0.015\times L^3$, where W=weight (g) and L=total length (cm).[1]

For each fish species, ten randomly selected otoliths from each stomach were measured (Murie, 1984). If fewer than ten suitable otoliths were present, all those available were utilized. Only otoliths with minimal degradation were measured. Degradation was apparent from a loss of detail, particularly the loss or reduction of spines and lobulations along the edges of the otoliths (Frost and Lowry, 1986).

Squid mantle lengths were estimated for each squid species by using linear regressions of mantle length on rostrum length and squid weights from regressions of $\log_e$ weight on $\log_e$ rostrum length (Wolff, 1984). Regressions were not available for patagonian squid, *Loligo gahi*, so regression equations for *Loligo opalescens*, a closely related species, were used (Wolff, 1984). For each squid species, ten randomly selected beaks were measured from each stomach, unless fewer than ten were present, in which case all were utilized.

A mean individual weight (MIW) was calculated for each prey species in each stomach and then used in estimating the percent weight contribution of each prey species to the dusky dolphin's diet. The MIW was usually the mean of the regression-estimated weights of individuals of a given prey species in a particular stomach, unless all hard parts were too degraded to permit reliable measurement, in which case an overall MIW, the mean of all regression-estimated lengths of that species in all stomachs with measurable hard parts, was employed. For anchoveta, however, enough measurable otoliths were available from stomach samples to permit statistical analyses by year and season of capture. Overall MIW's for anchoveta were therefore calculated for each group of stomachs within which analyses revealed no significant differences (for example, the summer of 1985; see Results).

The total weight of each species of squid or fish present in each dolphin stomach was estimated by multiplying the number of individuals present by the appropriate MIW value. The percent weight of each prey species in the dusky dolphin's diet was calculated by using weights summed over all stomachs, as 100 multiplied by the total weight of each prey species/the total weight of all prey present. Species for which regression-estimates of length and weight were not available were excluded from these calculations.

The percent gross energy contribution of each species was defined as 100 multiplied by gross energy of the prey species/summed gross energy of all prey consumed, for all stomach content samples. The gross energy available from a prey species is the caloric density ($kcal\cdot g^{-1}$)×weight (g) consumed. Caloric density (CD) values were obtained from the literature for each prey species, either directly from bomb-calorimetric analyses or indirectly from data on proximate composition, by using CD's for fat, carbohydrate, and protein of 9.4, 4.15, and 5.65 $kcal\cdot g^{-1}$, respectively (Pike and Brown, 1984).

By using published data from non-El Niño years only, CD values for anchoveta were calculated as 1.589 $kcal\cdot g^{-1}$ for the summer and 1.548 $kcal\cdot g^{-1}$ for the winter (Lam, 1968). Data were unavailable for *S. sagax*, but like *E. ringens* it is a clupeoid, and the reproductive seasons of the two species are similar (Muck et al., 1987; Pauly and Soriano, 1987), therefore *S. sagax* was assigned the same seasonal values as *E. ringens*. A value of 1.244 $kcal\cdot g^{-1}$ was calculated for *T. symmetricus* by using proximate composition values from the related *T. trachurus* (Sidwell, 1981). Similarly, a value of 1.158 $kcal\cdot g^{-1}$ for *M. gayi* was based on equivalent data from *M. productus* (Sidwell, 1981). For *Loligo gahi*, 0.968 $kcal\cdot g^{-1}$ was obtained from proximate composition data in Croxall and Prince (1982). No published values were available for *Dosidicas gigas*, so a mean ommastrephid

[1] Pauly, D. International Center for Living Aquatic Resources Management, Manila. Personal commun., 1985.

estimate of 0.922 kcal·g^{-1} was calculated from bomb calorimetric and proximate composition data in Croxall and Prince (1982), Vlieg (1984), and Clarke et al. (1985).

Statistical analyses

Seasonal and annual variation in the size of consumed anchoveta were analyzed with a two-way ANOVA of the mean estimated lengths of the anchoveta in each dolphin stomach, weighted by the number of otoliths measured (SAS, 1985 and 1987). Because of the unbalanced design, sums of squares and *F*-values were calculated by using the "Type III sum of squares" (SAS, 1985). Sidak adjusted *t*-tests were used for comparisons among pairs of means (Sokal and Rohlf, 1981; SAS, 1987). Log-linear analyses were conducted on frequency of occurrence data, also by using SAS (1987), and the resulting *G*-statistics were tested for significance following Sokal and Rohlf (1981).

Data from different locations were pooled for analyses of the effects of year and season on dusky dolphin feeding habits. This was appropriate because the two most distant of the three ports are separated by only about 160 km (Fig. 1), and all three ports are found along the central portion of the Peruvian coast. This region is relatively homogeneous and often treated as a single unit in analyses of oceanographic processes and fish populations (e.g. Brainard and McLain, 1987; Pena et al., 1989). It was necessary to pool data from all locations and collection periods to obtain sample sizes sufficient for analyses of prey occurrence with respect to dolphin reproductive status.

Results

One hundred and thirty-six stomach samples contained recognizable hard parts and were used in subsequent analyses (Table 1). Six additional stomachs were empty, containing no recognizable hard parts at the time of their collection. There were no obvious patterns in the years, seasons, or locations in which the empty stomachs occurred, or the reproductive status of the individuals from which they were obtained (Table 1). Eight additional samples contained otoliths at the time of their collection, according to field notes, but lacked otoliths when examined in the laboratory several months later. These otoliths may have dissolved during storage; therefore these samples were not included in analyses.

Species included in percent weight and percent gross energy calculations—*E. ringens, T. symmetricus, M. gayi, S. sagax, L. gahi* and *D. gigas*—represented the vast majority of prey, over 98% of the total number consumed. Other species, anchoa, *Anchoa* sp., blackruff, *Seriolella violacea*, a flyingfish, *Hirundichthys* sp., and deepsea smelt, *Leuroglossus urotramus*, were found in only trace amounts in stomach contents (Table 2).

Anchoveta was the most important prey species by all measures of relative importance. It accounted for 92.5% of all dusky dolphin prey items by total numbers and was present in 97.8% of stomachs. By weight, anchoveta accounted for 83.8% of prey, and by gross energy, 87.3% (Table 2). No other prey species accounted for more than 5.1% of prey by weight, 2.5% by total numbers, or 4.0% by gross energy, or was found in more than 26.5% of the stomachs examined (Table 2).

Table 1

Distribution of stomach content samples containing otoliths or squid beaks, or both, collected from dusky dolphins, *Lagenorhynchus obscurus*, by year, season, and dolphin reproductive status. Numbers in parentheses represent number of empty stomachs containing neither otoliths nor squid beaks.

			Reproductive status[1]							
Year	Season	Location	ImmF's	RestF's	PregF's	LactF's	UnknF's	Males	Unkn's	Total
1985	Summer	Pucusana	4	0	0	1	0	10	0	15
1985	Winter	Pucusana	0	0	0	1	0	0	0	1
1985	Winter	Ancon	4	7	0	8(1)	4	19(1)	0	42(2)
1986	Summer	Pucusana	1	1	3	5	0	10	0	20
1986	Summer	Cerro Azul	0	0	5	1	0	4(1)	0	10(1)
1986	Winter	Pucusana	4	5	4(1)	5	0	12(1)	4	34(2)
1986	Winter	Cerro Azul	1	2	6	1	0	4(1)	0	14(1)

[1] ImmF's=immature females; RestF's=resting females; PregF's=pregnant females; LactF's=lactating females (including simultaneously pregnant and lactating females; two were collected, one at Ancon in the winter of 1985, one at Pucusana in the summer of 1986); UnknF's=females of unknown reproductive status; Males=all males; Unkn's=individuals of unknown sex.

By weight, anchoveta accounted for more than half of all prey consumed in every collection period and its lowest frequency of occurrence was 93.3% (Table 3). The percent weight of *T. symmetricus* in dusky dolphin diets was always low, ranging from 0% in the winter of 1985 to a maximum of 14.5% in the summer of 1986, but frequency of occurrence was more variable, ranging from 0% to 53.3% (Table 3). In a log-linear analysis, the three-way interaction between year, season, and frequency of occurrence of *T. symmetricus* in stomachs was not statistically significant (G=1.91, df=1, P>0.10), nor was the interaction between season and frequency of occurrence significant (G=2.26, df=1, P>0.10). The large increase in frequency of occurrence of this prey from 1985 to 1986, however, resulted in a highly significant interaction between frequency of occurrence and year (G=37.76, df=1, P<0.001). The only other prey found sufficiently often in stomachs for statistical testing of frequency, but not so often that insufficient variation was present (as for anchoveta), was *L. gahi*, for which log-linear analysis yielded a significant three-way interaction between frequency of occurrence, year, and season of collection (G=13.44, df=1, P<0.001). Thus neither season nor year exerted a clear, independent effect on consumption of *L. gahi*, although there was considerable variation among collecting periods (Table 3).

Reproductive status did not have any obvious effect on dusky dolphin feeding habits (Table 4). The frequencies of occurrence of *T. symmetricus* and *L. gahi* did not differ significantly between either lactating females and pooled nonlactating mature females (G=0.39, df=1, P>0.5; G=1.06, df=1, P>0.3, respectively for each prey species) or between lactating females and all other individuals pooled (G=0.29, df=1, P>0.5; G=0.17, df=1, P>0.5, respectively). Anchoveta were consumed by both sexes almost without exception (Table 4).

Table 2

Relative importance of prey species of the dusky dolphin, *Lagenorhynchus obscurus*, from the coastal waters of central Peru in the summers and winters of 1985 and 1986 (n=136 stomachs, 9,137 individual fish and squid). Percent weight and percent gross energy were calculated by using only the six most important prey species.

Prey species	% Frequency of occurrence	% Total numbers[1]	% Weight	% Gross energy
Engraulis ringens	97.8	92.5	83.8	87.3
Trachurus symmetricus	26.5	2.5	3.5	2.9
Merluccius gayi	8.1	0.6	5.1	4.0
Sardinops sagax	4.4	0.2	2.2	2.3
Loligo gahi	19.1	2.2	3.7	2.4
Dosidicas gigas	11.0	0.4	1.6	1.0
Anchoa sp.	1.5	0.1	—	—
Seriolella violacea	1.5	0.0	—	—
Hirundichthys sp.	0.7	0.0	—	—
Leuroglossus urotramus	0.7	0.5	—	—
Unknowns[2]	9.6	1.1	—	—

[1] Percent total numbers values were sometimes very low, e.g. 0.01% or only 0.0% to an accuracy of one decimal place, even when a prey species was present in more than one stomach and its percent frequency of occurrence was greater than 1%.
[2] There appeared to be at least eight species of fish represented among the otoliths which could not be identified.

Table 3

Relative dietary contribution of prey species commonly eaten by the dusky dolphin, *Lagenorhynchus obscurus*, for each combination of year and season.

	% Total weight (% Frequency of occurence)			
Prey species	Summer 1985 (n=15)[1]	Winter 1985 (n=43)	Summer 1986 (n=30)	Winter 1986 (n=48)
E. ringens	76.6 (100.0)	86.4 (97.7)	66.0 (93.3)	91.4 (100.0)
T. symmetricus	0.2 (6.7**)	0.0 (0.0**)	14.5 (53.3**)	3.4 (39.6**)
M. gayi	22.0 (13.3)	3.1 (9.3)	6.9 (16.7)	0.0 (0.0)
S. sagax	1.0 (6.7)	0.4 (2.3)	0.9 (3.3)	4.9 (6.3)
L. gahi	0.1 (6.7**)	9.6 (34.9**)	2.3 (26.7**)	0.2 (4.2**)
D. gigas	0.0 (0.0)	0.5 (20.9)	9.4 (16.7)	0.1 (2.1)

[1] n=Number of dusky dolphins from which stomach content samples were collected.
** =Significant differences present at P<0.001.

Prey size

All dusky dolphin prey species for which lengths and weights could be estimated averaged less than 30 cm (mantle length for the squids, fork length for *M. gayi*, and total length for all others) and 300 g. The

Table 4

Percent composition by weight and frequency of occurrence of prey found in stomach contents of dusky dolphins, *Lagenorhynchus obscurus*, classified by reproductive status. All collection periods are pooled (summers and winters of 1985 and 1986).

		% Weight[2] (% Frequency of occurrence)					
Reproductive status[1]	*n*	*E. ringens*	*T. symmetricus*	*M. gayi*	*S. sagax*	*L. gahi*	*D. gigas*
Imm. Fem.'s	14	74.3	4.6	7.3	0.0	12.9	0.8
		(92.9)	(14.3)	(14.3)	(0.0)	(21.4)	(28.6)
Rest. Fem.'s	15	82.6	0.9	0.0	15.9	0.6	0.0
		(100.0)	(26.7)	(0.0)	(6.7)	(6.7)	(0.0)
Preg. Fem.'s	18	85.7	0.7	0.9	3.0	0.8	8.9
		(100.0)	(33.3)	(5.6)	(11.1)	(16.7)	(16.7)
Lact. Fem.'s	22	87.1	0.7	8.3	0.6	3.0	0.4
		(100.0)	(22.7)	(13.6)	(4.5)	(22.7)	(13.6)
Males	59	81.8	7.5	5.9	0.4	4.0	0.4
		(96.6)	(30.5)	(8.5)	(1.7)	(22.0)	(6.8)

[1] Imm. Fem.'s=immature females; Rest. Fem.'s=resting females; Preg. Fem.'s=pregnant females; Lact. Fem.'s=lactating females, including those simultaneously pregnant and lactating; Males=all males; individuals of unknown reproductive status omitted.
[2] May not total 100 in each row due to rounding.

most common prey species, *E. ringens*, *T. symmetricus*, and *L. gahi*, averaged less than 20 cm and 100 g (Table 5).

The regression-estimated lengths of consumed anchoveta varied significantly with year, season, and the interaction between year and season (F=416.06, 62.56, and 35.42, respectively; df=1, 67, $P \leq 0.0001$; Table 6). In comparisons between pairs of means, anchoveta were found to be significantly larger in the summer and the winter of 1986 than in either the summer or the winter of 1985 (Table 6). In 1985, otolith lengths were significantly different between summer and winter, but not in 1986 (Table 6).

Mean total lengths of anchoveta from fishery samples (for each combination of year and season) were positively correlated with mean regression-estimated lengths of anchoveta consumed by dusky dolphins (r=0.98, df=2, $P<0.05$; Table 6). Mean estimates of total length for anchoveta consumed by dusky dolphins were consistently 1.4–2.0 cm smaller than mean total lengths of anchoveta taken by the fishery, however (paired t-test, t=12.4, df=3, $P<0.01$).

Table 5

Mean lengths (cm) and weights (g), as estimated from regressions on otolith length/radius and squid beak rostrum length, of fish and squid species commonly found in the stomachs of the dusky dolphin, *Lagenorhynchus obscurus*, landed along the central Peruvian coast in 1985 and 1986.

	Estimated mean length (SE)		Estimated mean weight (SE)	
Prey species	No. of hard parts[4]	(No. of stomachs)[5]	No. of hard parts[4]	(No. of stomachs)[5]
E. ringens[1]	13.4	(0.14)	17.3	(0.49)
	593	(71)	593	(71)
S. sagax[1]	25.1	(0.32)	237.0	(8.67)
	4	(2)	4	(2)
M. gayi[2]	25.2	(4.62)	198.0	(104.0)
	18	(5)	18	(5)
T. symmetricus[1]	11.5	(1.16)	25.6	(8.67)
	34	(13)	34	(13)
L. gahi[3]	13.0	(0.27)	33.3	(1.23)
	97	(26)	97	(26)
D. gigas[3]	13.4	(1.00)	72.7	(16.4)
	34	(15)	34	(15)

[1] Total length.
[2] Fork length.
[3] Mantle length.
[4] Number of hard parts measured.
[5] Number of stomachs from which samples were taken.

Discussion

The prey of the dusky dolphin in Peruvian coastal waters can be characterized as schooling, small to medium size, pelagic or semi-pelagic species (*M. gayi* is usually demersal but sometimes forms large pelagic schools [Mejía and Jordán, 1979]). Anchoveta was typical and was unequivocally the most important prey species in 1985–86. It was most important by all measures of consumption and constituted almost 90% of the dusky dolphin's diet by percent gross

Table 6

Mean estimated total lengths of anchoveta, *Engraulis ringens*, consumed by dusky dolphins, *Lagenorhynchus obscurus*, in central Peruvian coastal waters in 1985 and 1986, compared to mean lengths of anchoveta taken in the purse-seine fishery.

Collection source	Summer 1985	Winter 1985	Summer 1986	Winter 1986
Stomachs of dusky dolphins				
Mean estimated total length of anchoveta[1] (SE)	11.5[a] (0.14)	12.9[b] (0.09)	14.1[c] (0.10)	14.3[c] (0.07)
Number of otoliths measured	112	150	103	228
Number of stomachs from which otoliths were collected	12	18	14	27
Purse-seine fishery				
Mean total length of anchoveta[2]	13.5	14.6	15.5	16.3

[1] Based upon measurements of otoliths in dusky dolphin stomachs.
[2] Mean total length of anchoveta taken in the fishery, calculated from data in Pauly and Palomares (1989); SE's and *N*'s unavailable.
[a,b,c] Means with different letters in the superscript differed significantly (Sidak adjusted *t*-tests; $t \geq 8.41$, $P < 0.001$ in all cases) while those with the same letter did not ($t = 1.42$, $P > 0.5$).

energy, usually considered the best measure of relative prey importance (Lavigne et al., 1982). Few data are available on feeding habits for other regions, but in Argentina dusky dolphins also fed on a species of anchovy (Würsig and Würsig, 1980).

There were no consistent seasonal patterns in prey consumption in the present study. Rather, anchoveta was the most important prey species in both seasons of both years, probably owing, in part, to its relatively high abundance throughout the study period (Pauly and Palomares, 1989). Consumption of *T. symmetricus* was more variable and opportunistic. In 1985 *T. symmetricus* was almost absent from stomach samples, but it was a major prey item in 1986 when unusually large numbers of juveniles, similar in size to other important dusky dolphin prey, were observed in the coastal waters of central and northern Peru (IMARPE et al., 1986). Other species, particularly *L. gahi*, varied greatly among collection periods in their importance as prey, but did not exhibit consistent seasonal or annual patterns.

In examining the effects of season, year, and other variables on diet, only frequency of occurrence was analyzed statistically because analyses of other measures of prey importance involve excessive violations of the assumptions underlying most statistical tests (Recchia and Read, 1989). Percent-weight estimates were used for qualitative comparisons among collection periods and reproductive classes, rather than percent gross energy values, because the latter were very gross approximations.

Anchoveta was the main prey of all reproductive classes of dusky dolphins. In contrast, in the eastern tropical Pacific most spotted dolphins, *Stenella attenuata*, eat mainly ommastrephid squids whereas lactating females eat principally fish (Bernard and Hohn, 1989). The greater energy and water requirements of lactating females may force them to feed on fish, which contain more energy and water per unit weight than squid or, alternatively, the presence of a calf may prevent females from feeding at the depths at which squid occur (Bernard and Hohn, 1989). In Peru, lactating dusky dolphins were apparently able to satisfy their energy and water requirements, as did other females, males and juveniles, by feeding on the abundant, high energy anchoveta (Lam, 1968).

Like the fishermen, fur seals, and seabirds of the Peruvian coast, dusky dolphins were somewhat opportunistic in their feeding in respect to the sizes of the anchoveta they preyed upon, taking more of the more abundant size classes (Muck and Pauly, 1987; Majluf, 1989). Anchoveta consumed by dusky dolphins were consistently 1.4–2.0 cm smaller, however, than those taken in the fishery, perhaps because of the fishery's bias towards larger anchoveta (Palomares et al., 1987). Alternatively, the slight degradation present in some of the otoliths from which anchoveta sizes were estimated may have resulted in underestimation of total lengths (Recchia and Read, 1989). The observed discrepancy may also be due to variation in the relationship between otolith size and body size, which can differ among years because of variation in growth rates of fish (McKinnon, 1988; Reznick et al., 1989; Secor and Dean, 1989; Campana, 1990).

Relative consumption of fishes with small otoliths, such as anchoveta, may have been underestimated. Large otoliths and squid beaks are less easily dissolved by stomach acids than are smaller otoliths (Hawes, 1983; Bigg and Fawcett, 1985; da Silva and

Neilson, 1985; Recchia and Read, 1989) and squid beaks are less easily passed through the digestive tract than are otoliths (Hawes, 1983; Bigg and Fawcett, 1985). This potential bias tends to strengthen the principal finding of this study: anchoveta was by far the most important prey species of all reproductive classes of Peruvian dusky dolphins in the summers and winters of 1985–86.

Acknowledgments

I was supported throughout this study by a scholarship from the Natural Sciences and Engineering Research Council (NSERC) of Canada. The research was funded by grants to David Gaskin (University of Guelph, Canada) from the United Nations Environmental Program and the International Union for the Conservation of Nature, and NSERC.

Andy Read, Julio C. Reyes, Koen Van Waerebeek, Linda Lehman, Maria Valle-Riestra, Steve Farnworth, and Mark Chandler assisted with field work. Without Julio Reyes, in particular, the project would have been much less successful. Patricia Majluf, Tony Luscombe, Leonardo Mendizabal Manrique, and the Farnworth, Malasquez, Reyes-Robles, Valle-Riestra, and Yonge families were hospitable and helpful in many ways. Jorge Zuzunaga, Marco Espino, and especially Juan Velez (all of IMARPE) provided much useful assistance and information. I thank the Capitania, Empresa Peruana de Servicios Pesqueros, and Ministerio de Pesqueria for allowing us to work in the fish markets.

Sue Candela identified many squid beaks, and Franz Cardoso was also instrumental in these identifications. Dan Ryan and O.B. Brian helped with statistics. Kenny Richard assisted with data input and checking. David Gaskin, Ronald Hardy, Linda Jones, Andy Read, and two anonymous reviewers provided many helpful comments on the manuscript.

Literature cited

Bernard, H. J., and A. A. Hohn.
1989. Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). J. Mamm. 70:211–215.

Bigg, M. A., and I. Fawcett.
1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 284–291. Allen and Unwin, London, 354 p.

Brainard, R. E., and D. R. McLain.
1987. Seasonal and interannual subsurface temperature variability off Peru, 1952–1984. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 14–45. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, Manila, 351 p.

Campana, S. E.
1990. How reliable are growth back-calculations based on otoliths. Can. J. Fish. Aquat. Sci. 47:2219–2227.

Chirichigno F., N.
1978. Clave para identificar los peces marinos del Perú. Informe Inst. Mar Perú-Callao 44, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 387 p.

Chirinos de Vildoso, A., and E. Chumán D.
1968. Validez de la lectura de otolitos para determinar la edad de la anchoveta (*Engraulis ringens*). Informe Inst. Mar Perú-Callao 22, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 34 p.

Clarke, A., M. R. Clarke, L. J. Holmes, and T. D. Waters.
1985. Calorific values and elemental analysis of eleven species of oceanic squids (Mollusca: Cephalopoda). J. Mar. Biol. Ass. U.K. 65:983–986.

Clarke, M. R. (ed.)
1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, 273 p.

Croxall, J. P., and P. A. Prince.
1982. Calorific content of squid (Mollusca: Cephalopoda). Br. Antarct. Surv. Bull. 55:27–31.

da Silva, J., and J. D. Neilson.
1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. 42:1439–1442.

Frost, K. J., and L. F. Lowry.
1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601–1607.
1986. Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea. Fish. Bull. 84:192–197.

Gaskin, D. E.
1972. Whales, dolphins and seals—with special reference to the New Zealand region. St. Martin's Press, New York, 200 p.
1982. The ecology of whales and dolphins. Heinemann, London, 459 p.

Goodall, R. N. P., and A. R. Galeazzi.
1985. A review of the food habits of the small cetaceans of the Antarctic and the sub-Antarctic. *In* W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic nutrient cycles and food webs, p. 566–572. Springer-Verlag, Berlin, 700 p.

Hawes, S. D.
1983. An evaluation of California sea lion scat samples as indicators of prey importance. Unpubl. M.A. thesis, San Francisco State Univ., 50 p.

IMARPE, SENAMHI, DHNM, and IGP.
1986. Condiciones bio-oceanográficas y meteorológicas frente a la costa Peruana en Enero-Junio 1986. ERFEN Boletín 19:3–11, Comisión Permanente del Pacífico Sur, Calle 76 No. 9, 88 Apartado Aereo 92292 Bogotá, Colombia.

Lam, R.
1968. Estudio sobre la variación del contenido de grasa en la anchoveta Peruana (*Engraulis ringens* J.). Informe Inst. Mar Perú-Callao 24, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 29 p.

Lavigne, D. M., W. Barchard, S. Innes, and N. A. Oritsland.
1982. Pinniped bioenergetics. *In* J. G. Clarke (ed.), Mammals in the seas, Vol. IV: small cetaceans, seals, sirenians and otters, p. 191–235. FAO Fisheries Series Number 5, Rome, 531 p.

Majluf, P.
1989. Reproductive ecology of South American fur seals in Peru. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 332–343. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

McKinnon, J. S.
1988. Feeding habits of three species of small cetaceans from the coastal waters of Perú. Unpubl. M.S. thesis, Univ. Guelph, 94 p.

Mejía G., J., and R. Jordán S.
1979. La situación actual del stock de merluza a setiembre de 1978. Informe Inst. Mar Perú-Callao 57, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 19 p.

Muck, P., and D. Pauly.
1987. Monthly anchoveta consumption of guano birds, 1953 to 1982. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 219–233. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Muck, P., O. Sandoval de Castillo, and S. Carrasco.
1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 268–275. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Murie, D. J.
1984. Estimating food consumption of free-living harp seals, *Phoca groenlandica* (Erxleben 1777). Unpubl. M.S. thesis, Univ. Guelph, 97 p.

Murie, D. J., and D. M. Lavigne.
1985. A technique for the recovery of otoliths from stomach contents of piscivorous pinnipeds. J. Wildl. Manage. 49:910–912.

Palomares, M. L., P. Muck, J. Mendo, E. Chumán, O. Gómez, and D. Pauly.
1987. Growth of the Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 117–141. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Pauly, D., and M. L. Palomares.
1989. New estimates of monthly biomass, recruitment and related statistics of anchoveta (*Engraulis ringens*) off Peru (4–14°S), 1953–1985. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 189–206. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

Pauly, D., and M. Soriano.
1987. Monthly spawning stock and egg production of Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 167–178. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Pauly, D., and I. Tsukayama (eds.).
1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Pauly, D., P. Muck, J. Mendo, and I. Tsukayama (eds.).
1989. The Peruvian upwelling ecosystem: dynamics and interactions. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

Peña, N., J. Mendo, and J. Pellón.
1989. Sexual maturity of Peruvian anchoveta (*Engraulis ringens*), 1961–1987. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 132–142. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

Perrin, W. F., and G. P. Donovan.
1984. Report of the workshop. Rep. Int. Whaling Comm. Spec. Issue 6:1–24.

Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holts.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. Fish. Bull. 71:1077–1092.

Pike, R. L., and M. L. Brown.
1984. Nutrition, an integrated approach, 3rd ed. John Wiley & Sons, New York, 1068 p.

Read, A. J., K. Van Waerebeek, J. C. Reyes, J. S. McKinnon, and L. C. Lehman.
1988. The exploitation of small cetaceans in coastal Peru. Biol. Cons. 46:53–70.

Recchia, C. A., and A. J. Read.
1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. Can. J. Zool. 67:2140–2146.

Reznick, D., E. Lindbeck, and H. Bryga.
1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 46:108–112.

Ryther, J. H.
1969. Photosynthesis and fish production in the sea. Science 166:72–76.

Samamé L., M.
1977. Determinación de la edad y crecimiento de la sardina *Sardinops sagax sagax* (J). Boletín Inst. Mar Perú-Callao 3:95–112. Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú.

SAS.
1985. SAS user's guide: statistics, version 5. SAS Institute, Cary, NC, 956 p.
1987. SAS/STAT guide for personal computers, version 6. SAS Institute, Cary, NC, 378 p.

Secor, D. H., and J. M. Dean.
1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Sidwell, V. D.
1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks and their products. Dep. Commer., NOAA Tech. Memo. NMFS F/SEC-11. Available from National Technical and Information Service, 5285 Port Royal Rd., Springfield, VA 22161, 440 p.

Sokal, R. R. and F. J. Rohlf.
1981. Biometry. W. H. Freeman and Company, New York, 859 p.

Treacy, S. D., and T. W. Crawford.
1981. Retrieval of otoliths and statoliths from gastrointestinal contents and scats of marine mammals. J. Wildl. Man. 45:990–993.

Van Waerebeek, K., and J. C. Reyes.
1990. Catch of small cetaceans at Pucusana port, central Peru, during 1987. Biol. Cons. 51:15–22.

Vlieg, P.
1984. Proximate composition of New Zealand squid species. N. Z. J. Sci. 27:145–150.

Wolff, G. A.
1984. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. Dep. Commer., NOAA Tech. Rep. NMFS 17. Available from National Technical and Information Service, 5285 Port Royal Rd., Springfield, VA 22161, 50 p.

Würsig, B., and M. Würsig.
1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fish. Bull. 77:871–890.

Distribution, abundance, and growth of larval walleye pollock, *Theragra chalcogramma*, in an Alaskan fjord

Franz-Josef Müter
Brenda L. Norcross
Institute of Marine Science, School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
Fairbanks, AK 99775-1080

Abstract.—This study examines the early life history of a population of walleye pollock, *Theragra chalcogramma* (Pallas), that is found in Resurrection Bay, Alaska. Ichthyoplankton samples were taken at six stations in Resurrection Bay during early May and early June 1989 along with hydrographic data. Standard lengths of all walleye pollock were measured, and subsamples from two stations were aged by using otolith increments for growth rate and hatch date analysis. Abundances ranged from 60 to 575 larvae m^{-2} in May and from 0 to 10 larvae m^{-2} in June with densities of up to 12 larvae m^{-3} in May. The estimated growth rate was 0.18 mm/day. Back-calculated hatch dates ranged from late March until early May; the median hatch date was 22 April. Comparisons of abundance and growth rate to values from other habitats indicate that this deep fjord provides a suitable habitat for larval walleye pollock. Hydrographic data and larval size distribution suggest that advection plays a major role in determining the distribution of larvae in the fjord.

Manuscript accepted 13 December 1993.
Fishery Bulletin 92:579–590 (1994).

Fjords have long been recognized as nursery grounds for many commercially important fish species (De Silva, 1973; Lie, 1978; Carmo Lopes, 1979). Matthews and Heimdal (1980) in their review of food chains in fjords pointed out that many fjords along Scandinavian, Scottish, and North American coasts are highly productive areas. The productivity of fjords is often enhanced by hydrographic boundary conditions or land runoff that can increase nutrient levels (Matthews and Heimdal, 1980). Production in fjords may be further enhanced by upwelling conditions at their mouths. This is especially true for the southern coast of Alaska, where the relaxation of easterly winds in summer promotes coastal divergence and upwelling (Royer, 1982).

Rogers et al. (1987) described the nearshore zone of the Gulf of Alaska as an important spawning or rearing area, or both, for several commercially important fish species, including walleye pollock, *Theragra chalcogramma*. However, no work has been done to examine the dynamics of early life history stages of walleye pollock or other fishes in Alaskan fjords.

We chose walleye pollock for this study because it was more abundant than any other species in Resurrection Bay (Smith et al., 1991) and its development and early life history in other areas of the Gulf of Alaska are well known (Dunn and Matarese, 1987; Kendall et al., 1987; Kim, 1989). Furthermore, it is very important commercially, with annual landings off Alaska exceeding one million metric tons (Lloyd and Davis, 1989), and the walleye pollock resource shows high fluctuations in year-class strength (Megrey, 1991), which creates a strong incentive to determine possible causes.

Most of the research on pollock in the Gulf of Alaska has been focused on the Shelikof Strait region (Schumacher and Kendall, 1991), while other areas along the Gulf, except for Auke Bay in Southeast Alaska (Haldorson et al. 1989, a and b), have received little attention. Although the Shelikof Strait spawning area is believed to be the most important in the Gulf of Alaska (Hinckley et al., 1991), substantial pollock spawning occurs in other areas of the Gulf (Müter, 1992; Norcross and Frandsen[1]).

Resurrection Bay shares many features with other embayments along the southcentral coast of Alaska and can be considered representative of the area. This study used growth analysis together with

[1] Norcross, B. L., and M. Frandsen. Distribution and abundance of larval fishes in Prince William Sound, Alaska, during 1989 after the *Exxon Valdez* oil spill. EVOS Symposium Proceedings. Am. Fish Soc. Symposium. In review.

distribution and abundance data to evaluate the role of this northern Gulf of Alaska fjord in the early life history of walleye pollock. Specifically, the objectives of this study were 1) to determine the distribution and abundance of walleye pollock larvae in a glaciated fjord, 2) to quantify growth rates of larvae within this fjord and compare growth rates to literature values from other areas, and 3) to estimate hatch dates of the observed population.

Materials and methods

Resurrection Bay is a fjord approximately 32 km long and 4–8 km wide, located within the coastal mountain range on the Kenai Peninsula on the south-central coast of Alaska (Fig. 1). The fjord's bathymetry shows an inner basin with a maximum depth of 300 m, separated by a sill from the outer basin. The sill is located about 15 km from the fjord's mouth at the narrowest point, between our sampling stations RES 2.5 and RES 3 (Fig. 1), and rises to a depth of approximately 185 m. The outer basin is slightly shallower (265 m) than the inner basin and has an open connection with the shelf.

Six stations were sampled along the fjord axis (Fig. 1) during two cruises, 1–4 May 1989 and 7–9 June 1989. Ichthyoplankton samples for this study were collected from the RV *Little Dipper*, a 9-m aluminum boat. Horizontal plankton tows were taken at discrete depths by using a 1-m^2 Tucker trawl, rigged with two 505-μ mesh nets. Because no previous data were available we took samples throughout the water column. We tried to obtain at least one sample from each of the following depth strata per station: 0–15 m, 15–30 m, 30–50 m, 50–80 m, 80–150 m, and 150-m to the bottom. Because of weather and time constraints, fewer samples were taken at some stations. Sample depths were initially estimated from wire angle and length of extended wire. Actual depths were recorded with an attached Seabird Seacat conducting-temperature-depth (CTD) (SBE 19) profiler and retrieved after completion of the cruise. The nets were rigged to a double tripper which allowed the second net to be opened and closed via a messenger from the surface. The net was towed for five minutes in the direction of tidal flow at a towing speed of 1.5 to 2.5 knots. Only daytime tows were made. Volume filtered during each tow was calculated from a TSK or General Oceanics flowmeter that was attached in a central position to the mouth of the net. Samples used for this analysis were immediately preserved in 50% isopropyl alcohol or 95% ethyl alcohol. The alcohol was renewed for each sample after 24 hours and after 2–3 days. Because differential shrinkage was observed between preservatives, only larvae preserved in isopropyl alcohol were used in size comparisons.

A Seabird CTD Profiler was attached to the net during most tows to record conductivity, temperature, and pressure throughout the tow. When no CTD data were recorded, depth was estimated from the wire angle and the length of extended wire. In addition, CTD data were taken at each station and along cross-fjord transects through each station. Because of equipment failure, no temperature and salinity data were obtained during the June cruise. Additional CTD-profiles for RES 2.5 and GAK 1 were obtained from a cruise on 6 April of the same year.

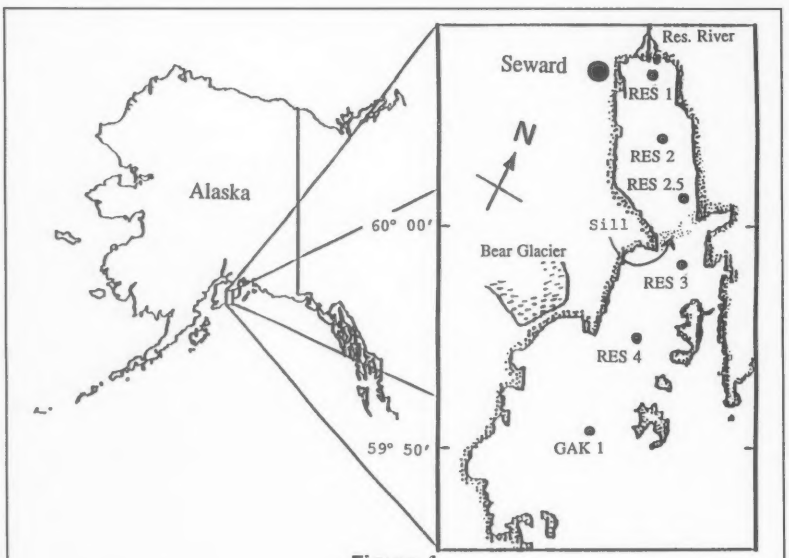


Figure 1
Map of Alaska and Resurrection Bay including stations sampled.

Samples were sorted in the laboratory to isolate finfish larvae. Walleye pollock larvae were identified and measured to standard length (SL). Densities in larvae·m^{-3} were calculated and abundance in larvae·m^{-2} at each station was estimated by integrating larval densities over the water column by using vertical distribution profiles. Density was set to zero at the surface and was assumed to change in a linear fashion between successive sampling depths. Be-

cause no replicate samples were taken, confidence limits could not be calculated.

A Student t-test (two-sample comparison) or a one-way ANOVA followed by a Tukey multiple comparison test (multiple samples) was employed to detect differences in mean standard length of larvae among different depths at the same station and among different stations. Nonparametric tests were employed in addition to parametric test procedures when the assumptions for parametric tests were violated. The nonparametric tests used were a Kruskal-Wallis test (nonparametric analysis of variance), a Mann-Whitney test (two-sample comparison), and a Tukey-type multiple comparison test (Zar, 1984).

Differences in larval length among stations were examined by using the most shallow samples from each station (<22 m), thus minimizing potential errors resulting from differences in size due to vertical distribution. In addition, pollock lengths from all depths were pooled for each station and the mean of the pooled data was compared between stations. For all between-station comparisons, larval mean SL was corrected for the date of sampling by using growth rates obtained during this study.

Ages of larvae were estimated from the number of otolith increments on sagittal otoliths as described in Kendall et al. (1987). Increments were independently counted a second time by the same reader. Readings were confirmed for a subsample of 20 otoliths by the Alaska Fisheries Science Center laboratory in Seattle, Washington. Only those independent readings that did not differ by more than one increment (in which case the higher count was used) were used for growth determination. Random subsamples of larvae from two stations, one in the inner basin (RES 2) and one in the outer basin (RES 4) were aged. Only larvae from these stations could be aged because otoliths from all other samples showed signs of erosion.

Larval growth rates were determined by fitting linear regression lines to length-at-age data. The linear regression equations describing growth were compared between stations to test for differences in regression coefficients. Slopes and elevations were compared by using Student's t-statistic (Zar, 1984). Hatch dates were estimated after correcting for mortality, because older fish in the sample experienced a higher cumulative mortality than larvae hatched closer to the date of sampling. Following Yoklavich and Bailey (1990), we created a stepped, size-specific mortality function with rates of 0.1, 0.08, 0.06, 0.03 per day for fish <7, 7.01–10.0, 10.01–15.0 and 15.01–20.0 mm SL, respectively. The range of ages corresponding to each size range was calculated from the growth equation obtained in this study. The hatch date distribution was then estimated by backcalculating numbers of larvae at hatching for each daily cohort with the above mortality rates.

Results

Hydrography of the fjord

On 6 April 1989, temperatures at RES 2.5 (inner basin) and GAK 1 (mouth of fjord) increased with depth from approximately 4°C in the surface layer to almost 6°C below 200 m (Fig. 2). Between April and May 1989 the properties of the water masses inside and outside the fjord changed considerably. In April the upper 100 m were nearly homogenous, but a strong seasonal thermocline had developed between 10 and 20 m in early May. The surface temperature in May varied between 5.8°C at RES 2.5 and 7°C at RES 3 (Fig. 2). Temperature profiles in May showed a pronounced minimum of about 3.5°C to 4.5°C near 80 m. While temperatures in April in

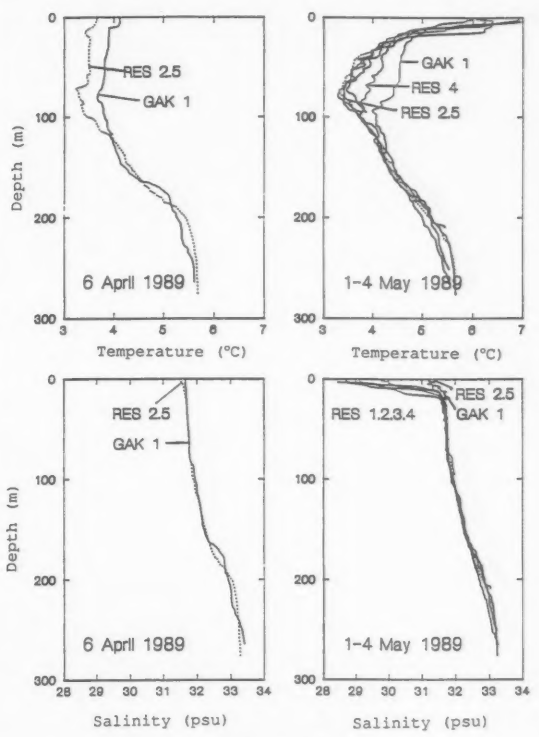


Figure 2

Temperature and salinity profiles at six stations in Resurrection Bay, Alaska, 6 April and 1–4 May 1989.

the upper 100 m did not differ by more than 0.5°C between RES 2.5 and GAK 1, the temperature difference in May was almost 1.5°C.

The water column was nearly isohaline in April: salinity increased approximately 1.5 psu (practical salinity unit) from surface to bottom. Salinity profiles in May show a well-developed low salinity surface layer at four of the stations (Fig. 2), resulting from river runoff and snow melt. The surface salinities were 2 to 4 psu lower than in April. However, at RES 2.5 and GAK 1 the freshwater lens was much less developed than at the other stations. The surface layer salinity was above 31 psu and almost identical at both stations. Below the halocline, salinities were very similar at all stations.

Distribution and abundance

In early May, walleye pollock larvae were caught at all stations and sampled at all depths. A total of 16,950 pollock larvae were collected in 39 tows at depths between 7 and 280 m. Larval densities ranged from 0.03 larvae·m^{-3} (RES 4, 105 m) to a maximum of 11.9 larvae·m^{-3} (RES 4, 26 m). Larvae were generally concentrated in the upper 70 m (Fig. 3). Maximum densities occurred at depths between 18 and 30 m at all stations, except GAK 1, and ranged from 2.2 larvae·m^{-3} to 11.9 larvae·m^{-3}. Pollock larvae were distributed deeper in the water column outside the sill, at stations RES 4 and GAK 1, than at stations inside the sill (Fig. 3).

Between May and June, larval densities decreased by two orders of magnitude and ranged from 0 to 0.4 larvae·m^{-3} in early June (Fig. 4). In June, a total of 420 walleye pollock larvae were collected in 45 tows at depths between 5 and 250 m. Only tows above 75 m caught pollock larvae. Vertically, the maximum in larval density occurred between 10 m (RES 1) and 58 m (RES 3). The vertical distribution in early June showed no apparent pattern in relation to station location (Fig. 4).

Using vertical distribution profiles, we estimated larval abundance at each station. In May, estimated abundances ranged from 60 larvae·m^{-2} at RES 1 to 575 larvae·m^{-2} at GAK 1 (Table 1). Abundances at the outer stations were much higher than in the inner basin owing to high larval densities below 50 m at RES 4 and GAK 1.

In June abundances ranged from 0.5 larvae·m^{-2} at RES 1 to 10.3 larvae·m^{-2} at RES 3. The estimated abundances were again higher at the outer stations. The highest abundance was found above the sill, as

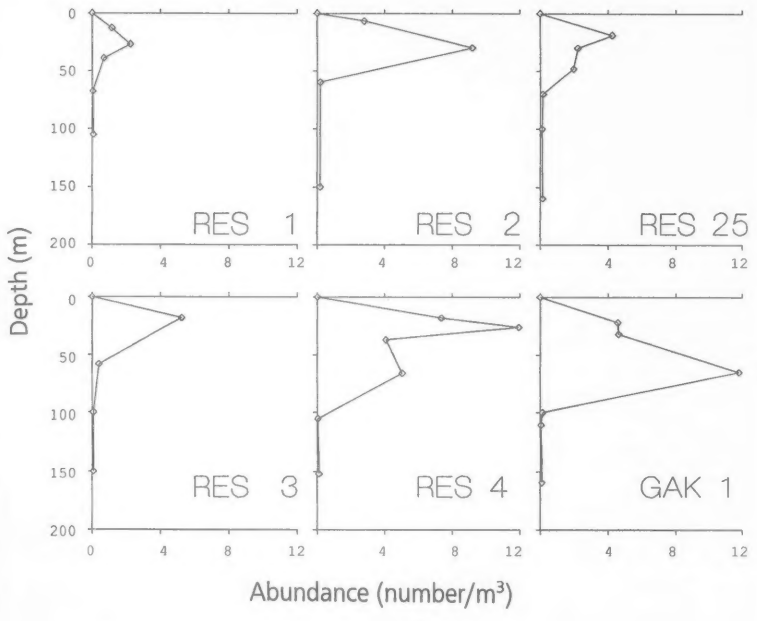


Figure 3

Vertical distribution of walleye pollock larvae, *Theragra chalcogramma*, in Resurrection Bay, Alaska, 1–4 May 1989.

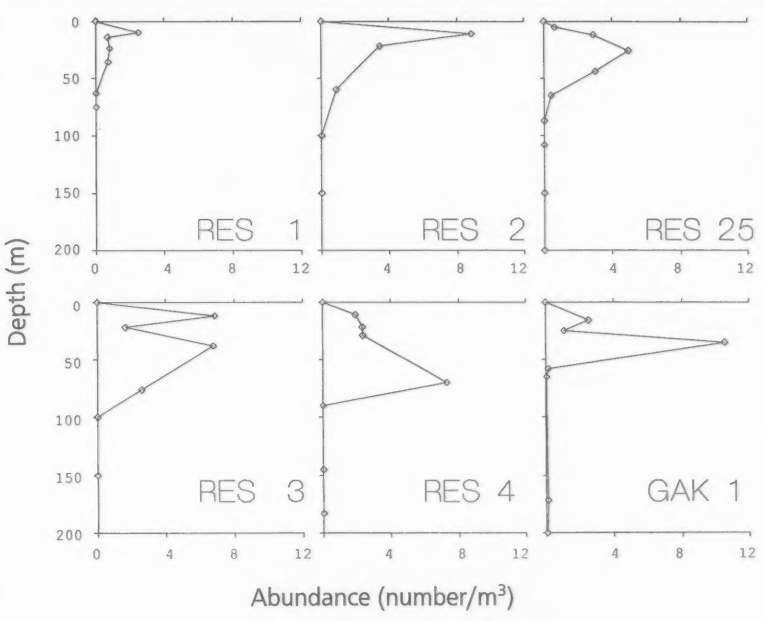


Figure 4

Vertical distribution of walleye pollock larvae, *Theragra chalcogramma*, in Resurrection Bay, Alaska, 7–9 June 1989.

the largest number of larvae was captured at RES 3 at 58 m. Abundance averaged across all stations decreased from 281 larvae·m^{-2} in early May 1989 to 4.6 larvae·m^{-2} five weeks later.

Larval size distribution

Mean SL of larvae differed significantly with depth at all stations in early May (Table 2). Both a *t*-test and a Mann-Whitney test of differences between means showed highly significant differences between the shallow and deep samples at RES 1, 2, 2.5, 3, and RES 4 ($P<0.01$). An ANOVA for station GAK 1 suggested highly significant differences as well ($F=42.33$; $P<0.001$). Results from a Tukey HSD test showed significant differences in mean standard length between the samples from 22 m and 65 m at GAK 1 ($P=0.01$). Differences between any of the remaining pairs at GAK 1 were not significant.

Table 1

Abundance of larval walleye pollock, *Theragra chalcogramma*, in Resurrection Bay in early May and early June 1989.

	Abundance (larvae·m^{-2})	
Station	May	June
RES 1	60	0.5
RES 2	285	4.0
RES 2.5	137	1.8
RES 3	168	10.3
RES 4	461	5.2
GAK 1	575	5.8

While significant differences in size with depth existed at all stations, the sign of the differences varied between stations. At the two innermost stations (RES 1 and RES 2) larval size decreased with depth, whereas at all other stations the opposite trend was found, i.e. larval size increased with depth, excluding the sample from 100 m at GAK 1. This sample showed a slight decrease in mean SL compared to shallower samples, but the difference was not significant.

To compare larval size between stations, mean SL was corrected for sample date by using observed growth rates. Since we sampled over a four-day period, the measured lengths differed because of growth during this period. Thus, standard length was corrected for date of sampling by using a growth rate of 0.18 mm/day, the overall growth rate of pollock larvae in Resurrection Bay (this study). Table 2 shows

mean SL, variance, and corrected mean SL for all samples collected in the upper 100 m. The corrected mean SL will be hereafter referred to as mean SL.

A nonparametric ANOVA by ranks showed that mean SL differed significantly between the shallow samples from each station (Kruskal-Wallis test statistic=746.5, $P<0.001$). A Tukey type nonparametric multiple comparison (Zar, 1984) indicated significant differences ($P<0.05$) between the innermost station pair (RES 1 and RES 2) and each of the stations outside RES 2 (RES 2.5, 3, 4, GAK 1). Among the outside stations, the only significant difference was found between RES 3 and GAK 1 ($P=0.003$).

When samples from all depths were pooled and mean SL compared between stations, results were very similar. An ANOVA showed a highly significant difference in mean SL between the stations ($F=80.00$, $P<0.001$). A Tukey HSD multiple comparison again indicated that significant differences ($P<0.05$) exist between both of the two innermost stations and any one of the stations outside RES 2.

Table 2

Range, mean, standard length (SL), variance, and mean SL corrected for date of sampling for larval walleye pollock, *Theragra chalcogramma*, collected in early May 1989 and preserved in isopropyl alcohol.

Station	Depth (m)	Number of larvae	Range (mm)	Mean SL (mm)	Variance	Corrected mean SL
RES 1	13	188	4.81–10.20	7.75	1.15	7.39
	39	91	4.49–9.31	6.81	0.85	6.45
RES 2	7	481	4.07–15.03	7.61	2.01	7.25
	60	24	4.59–8.40	6.67	1.02	6.31
RES 2.5	19	678	2.65–9.69	5.76	1.17	5.58
	90–110	36	5.22–8.93	6.50	0.62	6.32
RES 3	18	919	3.37–10.68	6.27	1.18	6.09
	58	95	4.15–9.58	6.91	0.88	6.73
RES 4	18	730	3.78–9.15	5.85	0.86	5.85
	66	735	3.58–8.31	6.09	0.50	6.09
GAK 1	22	983	2.87–8.81	5.37	0.78	5.55
	32	299	3.62–7.88	5.45	0.71	5.63
	65	2534	3.80–8.61	5.90	0.40	6.08
	100	29	4.31–6.84	5.65	0.37	5.83

Larvae at stations RES 1 and RES 2 were significantly larger and older than those at stations outside RES 2. The observed size differences translate into an age difference of 8.5 days between the average at the two inner stations (RES 1 and RES 2) and that at the outer stations (RES 2.5, 3, 4, and GAK 1). Age was calculated by using growth equations obtained in this study. The average age of larvae collected at stations RES 1 and RES 2 was estimated at 15.1 days. The average age of larvae at the other four stations was estimated to be 6.6 days, relative to 2 May. Thus, the results of size and age comparisons suggest that the stations can be divided into two distinct groups on the basis of larval size.

Growth rates

Growth rates were determined for larvae collected 1–4 May 1989 at station RES 2 in the inner basin and at station RES 4 in the outer basin. At station RES 2, 62 larvae collected at 7 m on 4 May 1989 were measured and dissected to remove otoliths, of which 54 could be aged. The increment count ranged from 6 to 40 increments for larvae between 5.1 mm and 11.1 mm SL. A linear regression model relating mean SL and increment count yielded a growth rate of 0.18 ± 0.028 mm/day (95% CI)($r^2=0.75$, Fig. 5), assuming each increment represents growth of one day. From a sample collected at RES 4, at 18 m on 2 May 1989, 38 larvae ranging in length from 5.3 mm to 10.1 mm were aged. The growth rate at this station was estimated to be 0.19 ± 0.016 mm/day ($r^2=0.79$, Fig. 5).

We compared the regression lines of standard length on increment count from RES 2 and RES 4 (Fig. 5) using the t-statistic according to Zar (1984) and found no significant difference between the slopes ($t=1.048$; $0.20<P<0.50$). This indicated that the growth rate was not different between the two stations. A common slope for both data sets was computed by using a weighted regression coefficient (Zar, 1984). The resulting combined growth rate for all walleye pollock larvae in Resurrection Bay was 0.18 mm/day.

In addition to length at age (increment count), we examined the relationships between otolith size and increment count and between otolith size and standard length. The regressions of otolith diameter on increment count resulted in a much tighter fit for both stations ($r^2=0.85$ for RES 2 and $r^2=0.91$ for RES 4; Fig. 6). Regressions of length on otolith size indicated a close relationship between body length and otolith diameter for the limited size range studied here ($r^2=0.83$ and $r^2=0.86$).

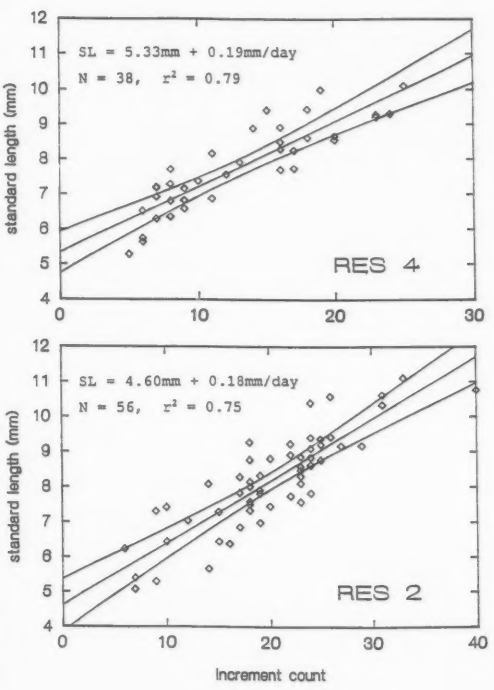


Figure 5

Linear regression of standard length on increment count for otoliths from larval walleye pollock, *Theragra chalcogramma*, at stations RES 2 and RES 4 in Resurrection Bay, Alaska.

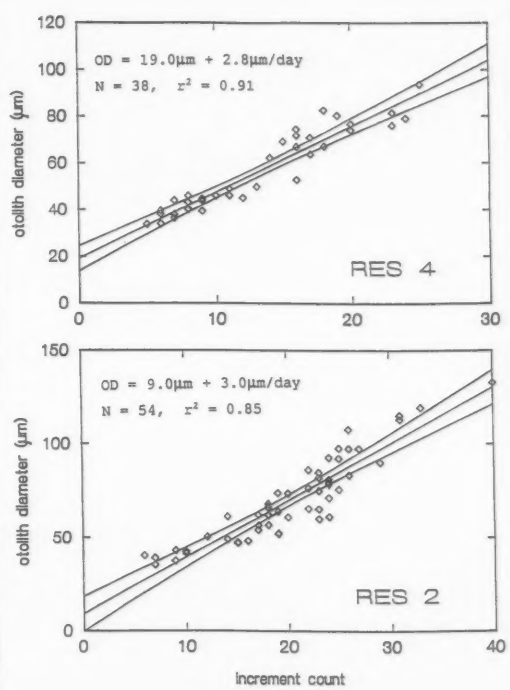


Figure 6

Linear regression of otolith diameter (OD) on increment count for otoliths from larval walleye pollock, *Theragra chalcogramma*, at stations RES 2 and RES 4 in Resurrection Bay, Alaska.

A comparison of elevations (y-intercept) of the two regression lines (Zar, 1984) also resulted in no significant difference (t=1.797; 0.05<P<0.10). Since the two subsamples used for ageing came from different preservatives, no common regression equation was computed. The regression equations relating length and age for larvae preserved in isopropyl alcohol was

$$SL = 4.60 \text{ mm} + 0.18 \text{ mm/day} \times \text{age(days)}.$$

Thus the following equation was used to convert length in isopropyl alcohol to ages:

$$\text{Age} = (SL - 4.60)/0.18.$$

Hatch dates

Estimated hatch dates for all larvae collected 1–4 May 1989 ranged from March 29 to May 9 with a median on 22 April (Fig. 7). Without mortality correction the median hatch date was 25 April.

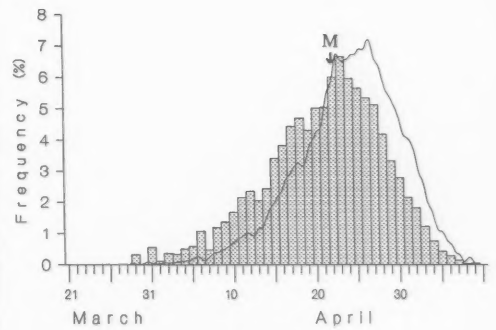


Figure 7

Estimated hatch date distributions of larval walleye pollock, *Theragra chalcogramma*, collected in Resurrection Bay, Alaska, 1–4 May 1989. Solid line shows hatch date distribution without mortality correction. "M" indicates median hatch date for mortality-corrected distribution.

Discussion

Distribution of pollock larvae in relation to hydrography

The vertical distribution of larval walleye pollock is influenced by behavioral responses to gravity, light, thermal stratification, turbidity, and turbulence (Olla and Davis, 1990). Even yolk-sac larvae are capable of oriented vertical movement. Olla and Davis (1990) found that larvae moved away from 3°C water in a vertical temperature gradient. Thus, temperature gradients may be reflected in the vertical distribution of walleye pollock larvae.

The results of this study show that the vertical distribution of walleye pollock larvae differed between the inner and the outer basin of Resurrection Bay in May 1989. Larvae at the outermost stations, RES 4 and GAK 1, were distributed deeper in the water column (Fig. 3). This is consistent with an upward migration of young larvae after hatching. Larvae are significantly younger at the outer stations and are distributed deeper in the water column and closer to the depth of hatching. Alternatively, larvae may select a preferred temperature by avoiding layers of cold water. Water temperatures below 40 m were about 1°C warmer at GAK 1 than at all stations inside the sill (Fig. 2). Temperatures at RES 4, located between GAK 1 and the sill, were intermediate. Cold water of less than 4°C below 40 m in the inner basin might prevent larvae from descending in the water column, resulting in the observed shallow distribution.

The horizontal distribution of larvae is largely determined by upper layer flow. Surface inflow of water into Resurrection Bay has been observed in acoustic doppler current profiler (ADCP) transects across the fjord, and average flow at 15 m depth at a mooring location above the sill was up-fjord between June and October 1989 (Weingartner[2]). If the water in this layer flowed up the fjord during April and May, it would provide a mechanism for advection of larvae into Resurrection Bay. Inflow of water at 15 m requires a compensating outflow. If the upper layer flow is divided in the horizontal plane with inflow on one side of the fjord and outflow on the other side, larvae may simply be transported through the fjord and their residence time could be very short. Alternatively, if surface inflow is compensated for by subsurface outflow or outflow in a shallow low-salinity surface layer, larvae could accumulate inside the fjord if they maintain their vertical position in the water column.

The available evidence suggests that the former mechanism, i.e. two-way surface flow, dominates in the outer fjord basin. The relatively high surface salinity at GAK 1 suggests that the water in the outer basin originates on the shelf. A salinity transect across GAK 1 shows relatively low salinities at both ends of the transect and higher salinities in the center. This does not imply, but is consistent with, an inflow of water along the east side of the outer fjord basin and an outflow along the western shore. Inflow of nearshore water along the eastern shore into Resurrection Bay can be seen in satellite images of the area (Royer[3]) and there is evidence from ADCP transects for a counterclockwise circulation in the outer basin (Weingartner[4]). Larvae that originate on the shelf thus may be carried counterclockwise through the outer basin. Larvae could be carried into the inner fjord by intrusions of surface water across the sill. We probably observed such an intrusion between 1 and 3 May 1989 (Müter, 1992).

It has been demonstrated for several fjords in Norway that water exchange processes can have a profound influence on the community structure within fjords (Lindahl and Perissinotto, 1987). Advective processes can even be the major factor regulating zooplankton biomass in a fjord (Lindahl and Hernroth, 1988). Advection of plankton into Resurrection Bay from the shelf is evidenced by the fact that in addition to resident nearshore species like *Pseudocalanus* spp., oceanic copepods (*Calanus* spp.) common in the Alaska Coastal Current, are found in high concentrations inside the fjord (Smith et al., 1991). Larval walleye pollock found inside Resurrection Bay could similarly originate on the shelf and enter the fjord as a result of advective processes. Plankton samples collected in 1991 suggest that larvae entered the fjord from outside (Müter, unpubl. data). However, acoustic surveys indicated the presence of adult walleye pollock inside Resurrection Bay in the spring of 1983 and at least some spawning may occur inside the fjord (Paul[5]).

Abundance

Our results indicate that walleye pollock larvae were abundant in Resurrection Bay and on the shelf outside Resurrection Bay, as represented by GAK 1. High densities of larval pollock up to 55 larvae·m^{-3} were

[2] Weingartner, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775–1080. Unpubl. data, 1989.

[3] Royer, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775–1080. Personal commun., 1992.

[4] Weingartner, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775–1080. Personal commun., 1992.

[5] Paul, A. J. Seward Marine Center, Institute of Marine Sciences, Box 730, Seward, AK. Personal commun., 1992.

also observed in nearby Prince William Sound in May 1989 (Norcross and Frandsen[1]). Larval concentrations inside the fjord in early May 1989 approached those found in the dense larval patch in Shelikof Strait in some years. In most years abundances of early larvae in Shelikof Strait range from 0 to 1,000 larvae·m^{-2} (Kendall et al., 1987; Kendall and Picquelle, 1990), compared with 60–575 larvae·m^{-2} in this study. However, in peak years, abundances in Shelikof Strait exceed the 1989 estimates for Resurrection Bay by one to two orders of magnitude, with 10,000 larvae·m^{-2} in 1981 (Bates and Clark[6]). Larval concentrations in Funka Bay, Japan, decrease from >5,000 larvae·m^{-2} at some stations in January to 200–400 larvae·m^{-2} in early April (Nakatani, 1988). For the Bering Sea, typical abundance estimates range from 10 to 100 larvae·m^{-2} distributed over a very large area (Incze et al., 1984). In Auke Bay, Alaska, the observed abundances were much lower with maximum densities of 3–15 larvae·m^{-2} (Haldorson et al., 1989a).

In ichthyoplankton samples taken in Resurrection Bay in the upper 30 m in 1988, maximum densities ranged from 0.8 larvae·m^{-3} at RES 1 to 4.1 larvae·m^{-3} at RES 4 (Smith et al., 1991), translating into abundances per unit area of 24 larvae·m^{-2} and 124 larvae·m^{-2} respectively. However, these abundances may be underestimates, since only the upper 30 m were sampled by Smith et al. (1991), whereas our study found high abundances below 30 m, particularly in the outer basin of the fjord (Fig. 3). Additional samples were collected in Resurrection Bay in late April and early May 1991. Abundances were similar to those estimated for 1989 (Müter, unpubl. data). The available data from 1988 to 1991 suggest that larval walleye pollock are consistently found in Resurrection Bay. The observed abundances are close to those resulting from the dense spawning aggregations found in Shelikof Strait, Alaska, and Funka Bay, Japan (Kendall and Nakatani, 1992). Since the spatial extent of the spawning area in the vicinity of Resurrection Bay is unknown, total abundances cannot be compared at present.

[6] Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaskan Peninsula during spring 1981. NWAFC Proc. Rep. 83–89. Northwest and Alaska Fisheries Sci. Center, NMFS, NOAA, Seattle, WA, 105 p.

Larval size and age distribution

Larvae from the shallowest samples at stations RES 1 and RES 2 were significantly larger and older than those at the other stations. Larvae from the shallowest tows may not be representative of the population as a whole because of changes in vertical distribution with age. Thus we also pooled larvae from all tows at each station for between-station comparisons. Some bias may remain because of inconsistencies in the depth sampling regime, but the results were almost identical to those obtained when only shallow samples are used. There is clearly a difference in size and age between larvae at stations RES 1 and RES 2 and larvae at all other stations. This observation is consistent with the hypothesis that larvae are transported into the fjord and accumulate inside the inner fjord basin. A length-frequency distribution for all larvae collected at each station (Fig. 8) shows a multimodal length distribution and

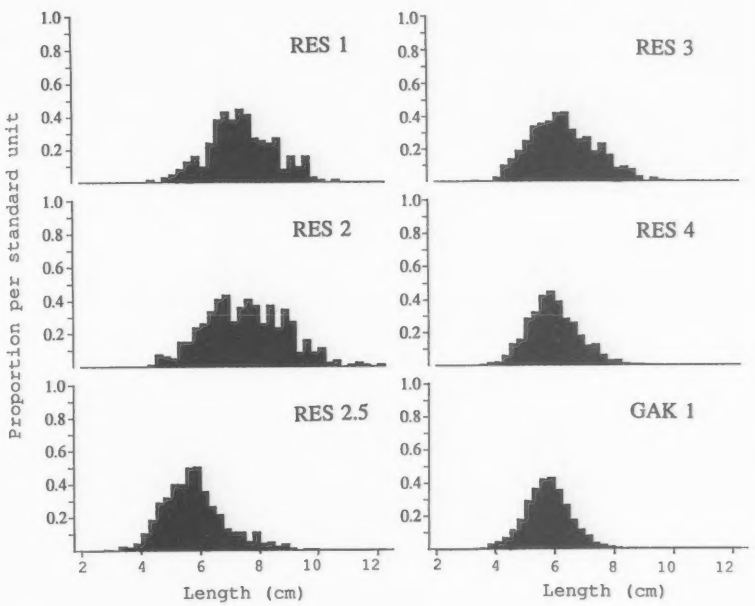


Figure 8

Length-frequency distributions of all larval walleye pollock, *Theragra chalcogramma*, captured at six stations in Resurrection Bay, Alaska, 1–4 May 1989.

a wide range of measured lengths at both RES 1 and RES 2, whereas at all other stations they show a more narrow, unimodal distribution. This distribution could be the result of several intrusions of surface water and larvae into the inner fjord.

Growth

The growth rates in Resurrection Bay were close to those reported for larvae from other geographic areas (Table 3), including Shelikof Strait and Auke Bay, which are located in the Gulf of Alaska at latitudes similar to Resurrection Bay. Temperatures in the upper layer in Resurrection Bay were slightly lower in early May 1989 than those observed in Shelikof Strait and Auke Bay at the same time of year (Kendall et al., 1987; Pritchett and Haldorson, 1989; Fig. 2). The low temperatures in the inner basin in May reflect delayed warming of the upper water column relative to the shelf outside the fjord. Thus, it may seem that the fjord in early spring provides less favorable conditions for growth than the shelf, considering the lower temperatures inside the fjord. However, salinities also differ between the shelf and the fjord, resulting in a more pronounced stratification inside Resurrection Bay. Stratification of the water column will reduce vertical mixing and can result in an earlier onset of phytoplankton and zooplankton blooms. In spite of differences in temperature, stratification, and vertical distribution (Kim, 1989; Pritchett and Haldorson, 1989), growth rates are very similar in Shelikof Strait, Auke Bay, and Resurrection Bay.

We detected no difference in growth rate between stations RES 2 and RES 4 in Resurrection Bay. This result is not surprising, given the proximity of the stations and the similarity in water properties. The growth rates, especially at the outer station, may be biased because only fish from the shallowest samples were aged. Larvae from the upper layer may not adequately represent the whole population. More samples would be needed to accurately test for differences in growth between stations. To test for interannual differences, data from additional years are needed. Differences in growth rates are most commonly attributed to variations in water temperature and prey concentration. The primary prey of first feeding walleye pollock are copepod nauplii ranging in length from 100 to 300 μm (Kamba, 1977; Clarke, 1978). Smith et al. (1991) found over 20 copepod nauplii (150–350 μm length) per liter throughout May 1988 in Resurrection Bay with numbers exceeding 100 per liter in mid-May. These prey concentrations are sufficient for successful feeding of larval walleye pollock (Paul, 1983; Haldorson et al., 1989b). Under these conditions growth of larvae in Resurrection Bay is not food limited. Growth rates in Resurrection Bay were also similar to those observed in the laboratory under optimal feeding conditions and at a higher temperature (Bailey and Stehr, 1988), further suggesting that growth was not food or temperature limited.

Many studies have documented the effects of water temperature on growth of fish larvae (Houde, 1989). Laboratory studies have shown that first-feeding walleye pollock larvae reared at 5.5°C are more successful at capturing prey than larvae reared at 3°C (Paul, 1983). Brown and Bailey (1992) found geographical differences in growth for juvenile walleye pollock that could be attributed to differences in temperature as well as nutrient levels. In our study, temperatures in the larval environment ranged from 3.5 to 6.3°C and growth rates fall well within the observed range of growth in other habitats.

Hatching and spawning

Hatch dates in Resurrection Bay fall well within the range of observed hatch dates in other parts of the

Table 3

Laboratory and field-estimated growth rates of larval walleye pollock, *Theragra chalcogramma*.

Year	Location	Size range (mm)	Temperature range (°C)	Growth rate (mm/day)	Reference
1981	Shelikof Strait	3–13	no data	0.17	Kim and Gunderson (1989)
1983	Shelikof Strait	6–15	5.5–7	0.21	Kendall et al. (1987)
1986	Auke Bay	4–13	6–7	0.23	Haldorson et al. (1989a)
1987	Auke Bay	5–11	5.5–7	0.16	Haldorson et al. (1989a)
1988	Auke Bay	5–11	6–7	0.22	Haldorson et al. (1989a)
1989	Auke Bay	5–12	4–6.5	0.18	Haldorson et al. (1989a)
	Laboratory	4–11	9.3±0.5	0.20	Bailey and Stehr (1986)
	Laboratory	4–10	8–9	0.18	Bailey and Stehr (1988)
	Resurrection Bay	3–15	3.5–6.3	0.18	This study

Table 4

Median hatch dates of larval walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska.

Year	Location	Hatch date	Reference
1983	Shelikof Strait	23 April	Yoklavich and Bailey (1990)
1985	Shelikof Strait	23 April	Yoklavich and Bailey (1990)
1986	Shelikof Strait	29 April	Yoklavich and Bailey (1990)
1987	Shelikof Strait	2 May	Yoklavich and Bailey (1990)
1987	Auke Bay	28 April	Haldorson et al. (1989a)
1989	Resurrection Bay	22 April	This study

Gulf of Alaska (Table 4). The median hatch date is remarkably consistent among different parts of the Gulf and among different years which would require a common, underlying mechanism to trigger spawning over such a broad geographical range. The values from Shelikof Strait suggest a trend towards later spawning dates between 1983 and 1987. More data are needed to determine if a similar trend exists in other areas of the Gulf and to identify parameters responsible for the timing of spawning.

Conclusions

The high abundances and growth rates of larvae in Resurrection Bay indicate that the fjord provides a suitable environment for the successful growth of larval walleye pollock. The hydrography of the region and larval size distributions support the hypothesis that larvae recruit to the fjord from outside by advection into the outer basin of Resurrection Bay and across the sill. These observations and the high abundances of pollock larvae in nearby Prince William Sound during the same year (Norcross and Frandsen[1]) suggest that a large spawning population of walleye pollock exists in the region and that not all walleye pollock in the northern Gulf of Alaska spawn in Shelikof Strait. Larval walleye pollock are also abundant in the bays of Southeast Alaska (Haldorson et al., 1989, a and b). Thus, it is likely that many embayments along the Gulf of Alaska are utilized by this species.

Future work is needed to determine the extent of spawning in the vicinity of Resurrection Bay and Prince William Sound and to test whether the area is consistently used by larval walleye pollock or whether abundances observed in 1989 were unusual. Also, the residence time of larvae in the area is not known. While larval pollock were found in Resurrection Bay in all three years for which data are available, there has been only one report of juvenile walleye pollock in the fjord (Feder et al., 1979).

Acknowledgments

We thank T. Weingartner and T. Royer for the use of unpublished data, B. Holladay and A. J. Paul for review of the manuscript, and A. L. Brown, K. M. Bailey, K. Besser, and L. Haldorson for help with larval otolith ageing. Two anonymous reviewers provided helpful suggestions. Funding for this study was provided by Alaska Sea Grant No. NA86AA-D-56041.

Literature cited

Bailey, K. M., and C. L. Stehr.
1986. Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. exp. Mar. Biol. Ecol. 99:233–246.
1988. The effects of feeding periodicity and ration on the rate of increment formation in otolith of larval walleye pollock, *Theragra chalcogramma*, Pallas. J. exp. Mar. Biol. Ecol. 122:147–161.

Brown, A.L., and K. M. Bailey.
1992. Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. Mar. Biol. 112:23–30.

Carmo Lopes, P. do.
1979. Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. Sarsia 64:199–210.

Clarke, M. E.
1978. Some aspects of the feeding biology of larval pollock, *Theragra chalcogramma* (Pallas), in the southeastern Bering Sea. M.S. thesis, Univ. of Alaska, Fairbanks, Alaska, 44 p.

De Silva, S. S.
1973. Abundance, structure, growth and origin of inshore clupeid populations of the west coast of Scotland. J. exp. Mar. Biol. Ecol. 12:119–144.

Dunn, J. R., and A. C. Matarese.
1987. A review of the early life history of northeast Pacific gadoid fishes. Fish. Res. 5:163–184.

Feder, H. M., A. J. Paul, and J. McDonald.
1979. A preliminary survey of the benthos of Resurrection Bay and Aialik Bay, Alaska. Sea Grant Report 79-9. Alaska Sea Grant Program, Fairbanks, Alaska, 53 p.

Haldorson, L., A. J. Paul, D. Sterritt, and J. Watts.
1989a. Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaskan bay. Rapp. P.-v. Reun. Cons. int. Explor. Mer 191:220–225.

Haldorson, L., J. Watts, D. Sterritt, and M. Pritchett.
1989b. Seasonal abundance of larval walleye pollock in Auke Bay, Alaska, relative to physical factors, primary production, and production of zoo-

plankton prey. *In* Alaska Sea Grant Report 89-1, p. 159–172.

Hinckley, S., K. M. Bailey, S. J. Picquelle, J. D. Schumacher, and P. J. Stabeno.
1991. Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 48:91–98.

Houde, E. D.
1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87:471–495.

Incze, L. S., M. E. Clarke, J. J. Goering, T. Nishiyama, and A. J. Paul.
1984. Eggs and larvae of walleye pollock and relationships to the planktonic environment. *In* D. H. Ito (ed.), Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea, p. 109–159. NOAA Tech. Memo. NMFS F/NWC-62.

Kamba, M.
1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175–197.

Kendall, A. W., Jr., and S. J. Picquelle.
1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish. Bull. 88:133–154.

Kendall, A. W., Jr., and T. Nakatani.
1992. Comparisons of early-life-history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido, Japan. Fish. Bull. 90:129–138.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Kim, S.
1989. Early life history of walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska. *In* Alaska Sea Grant Report 89-1, p. 117–139.

Kim, S., and D. R. Gunderson.
1989. Cohort dynamics of walleye pollock in Shelikof Strait, Gulf of Alaska, during egg and larval periods. Trans. Am Fish. Soc. 118:264–273.

Lie, U.
1978. Eggs and larvae of fish from Lindaspollene. Sarsia 63(3):163–167.

Lindahl, O., and R. Perissinotto.
1987. Short-term variations in the zooplankton community related to water exchange processes in the Gullmar Fjord, Sweden. J. Plankton Res. 9:1113–1132.

Lindahl, O., and L. Hernroth.
1988. Large-scale and long-term variations in the zooplankton community of the Gullmar Fjord, Sweden, in relation to advective processes. Mar. Ecol. Prog. Ser. 43:161–171.

Lloyd, D. S., and S. K. Davis.
1989. Biological information required for improved management of walleye pollock. *In* Alaska Sea Grant Report 89-1, p. 9–31.

Matthews, J. B. L., and B. R. Heimdal.
1980. Pelagic productivity and food chains in fjord systems. *In* H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), Fjord oceanography. Plenum Press, New York, p. 377–397.

Megrey, B. A.
1991. Population dynamics and management of walleye pollock *Theragra chalcogramma* in the Gulf of Alaska, 1976–1986. Fish. Res. 11:321–354.

Müter, F. J.
1992. Distribution, abundance, and growth of larval walleye pollock (*Theragra chalcogramma*) in an Alaskan fjord. M.S. thesis, Univ. Alaska Fairbanks, 91 p.

Nakatani, T.
1988. Studies on the early life history of walleye pollock in Funka Bay and vicinity, Hokkaido. Mem. Fac. Fish., Hokkaido Univ. 35:1–46.

Olla, B. L., and M. W. Davis.
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105–112.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Pritchett, M., and L. Haldorson.
1989. Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*). *In* Alaska Sea Grant Report 89-1, p. 173–183.

Rogers, D. E., B. J. Rogers, and R. J. Rosenthal.
1987. The nearshore fishes. *In* D. W. Hood and S. T. Zimmerman (eds.), The Gulf of Alaska, physical environment and biological resources. Mineral Management Service OCS study MMS 86-0095, p. 399–416.

Royer, T. C.
1982. Coastal freshwater discharge in the northeast Pacific. J. Geophys. Res. 87:2017–2021.

Schumacher, J. D., and A. W. Kendall Jr.
1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. CalCOFI Rep., Vol. 32, p. 22–40.

Smith, R. L., A. J. Paul, and J. M. Paul.
1991. Timing and abundance of herring and other fish larvae in an Alaskan glaciated fjord. *In* Proc. int. herring symposium Oct. 1990, Anchorage, Alaska. Alaska Sea Grant Report 91-01.

Yoklavich, M. M., and K. M. Bailey.
1990. Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis. Mar. Ecol. Prog. Ser. 64:13–23.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, New Jersey, 718 p.

Interannual variation in the recruitment pattern and abundance of age-0 summer flounder, *Paralichthys dentatus*, in Virginia estuaries*

Brenda L. Norcross

Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062
Present address: Institute of Marine Science
School of Fisheries and Ocean Sciences, University of Alaska Fairbanks
Fairbanks, Alaska 99775-1080

David M. Wyanski

Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062
Present address: South Carolina Marine Resources Research Institute
South Carolina Wildlife and Marine Resources Department
P.O. Box 12559, Charleston, South Carolina 29422

Abstract.—Capture of transforming larval and newly settled juvenile (age-0) summer flounder, *Paralichthys dentatus*, over four years (1986–1989) in the seaside salt marshes of Virginia's Eastern Shore and in the lower Chesapeake Bay verifies Virginia waters as a nursery area. Gear specific for juvenile flatfish was used and sampling was conducted in a broad range of habitats in all months. This study demonstrates a fluctuation in the timing of the appearance and magnitude of abundance of age-0 summer flounder in Virginia waters over a four-year sampling period. Age-0 summer flounder (11–27 mm TL) began entering the area in October 1986 and were present throughout the winter of 1987. The 1988 and 1989 year classes did not appear until April at larger sizes (22–83 mm TL). Highest catch per unit of effort (CPUE) occurred between April and August and abundance declined in the fall. Data indicated that year-class strength declined from 1986 to 1988 and increased slightly in 1989. To monitor year-class strength of age-0 summer flounder, we recommend sampling Virginia estuaries in April, May, and June when both abundance of flounder is high and small-mesh-lined trawl gear is most efficient.

Summer flounder, *Paralichthys dentatus* (Pleuronectiformes: Bothidae), is an important commercial and recreational species along the eastern coast of the United States. It ranges from Nova Scotia (Scott and Scott, 1988) to Florida (Gutherz, 1967) and its center of abundance occurs in the Middle Atlantic Bight (Scarlett, 1981). Though it is known that commercial landings of *P. dentatus* in the Middle Atlantic Bight fluctuate widely (Wilk et al., 1980), fluctuations in abundance of age-0 summer flounder have not been investigated. Because of the economic importance of summer flounder in Virginia, our first objective was to design a sampling plan based on the early life history of summer flounder to assess the relative yearly abundance of age-0 summer flounder in Virginia waters. This index will provide the fishing industry and fishery managers with knowledge of fluctuations before those fluctuations affect the fishery. A part of designing an effective sampling plan was evaluation of appropriate gear. Therefore, the second objective was to examine the effectiveness of sampling gear.

Age-0 *P. dentatus* have been captured in small numbers from Chesapeake Bay (Orth and Heck, 1980; Weinstein and Brooks, 1983) and the Eastern Shore of Virginia (Richards and Castagna, 1970). Poole (1966) hypothesized that Virginia waters and the sounds of North Carolina constitute primary nursery areas for summer flounder, but an insufficient number of specimens have been captured to substantiate this hypothesis. Recruitment and distribution patterns of age-0 summer flounder have been investigated in estuaries in North Carolina (Powell and Schwartz, 1977; Miller et al., 1984; Burke et al., 1991)

Manuscript accepted 16 December 1993.
Fishery Bulletin 92:591–598 (1994).

* Contribution 1748 from the Virginia Institute of Marine Science.

and New Jersey (Able et al., 1990); however, the studies in Virginia reporting the capture of age-0 summer flounder were not directed specifically at this species (Richards and Castagna, 1970; Orth and Heck, 1980; Weinstein and Brooks, 1983). Thus the third objective of this study was to assess the region's importance as a nursery area.

Methods

Sampling sites were located on the seaside (eastern border) and bayside (western border) of Virginia's Eastern Shore and on the western shore of Chesapeake Bay (Fig. 1) because the Chesapeake Bay and Eastern Shore were hypothesized to be prime nursery grounds (Poole, 1966). The eastern border of the Eastern Shore peninsula is an extensive system of barrier islands enclosing salt marshes and shallow bays that are 1–2 m deep at mean high water (MHW). The bays and salt marshes are transected by main channels that are 3–20 m deep at MHW. On the western border of the peninsula, there are shallow creeks, 1–6 m deep at MHW, which extend into upland areas. Fringing and pocket marshes, much less extensive than the seaside salt marshes, occur along creek margins. Seagrass beds are present at the mouth of most creeks. The mouth of the York River (Fig. 1) is 3.7 km wide; it has extensive shoal areas along its margins and a main channel 18 m deep. Salt marshes, with channels 1–3 m deep, and seagrass beds are present in the shoal areas.

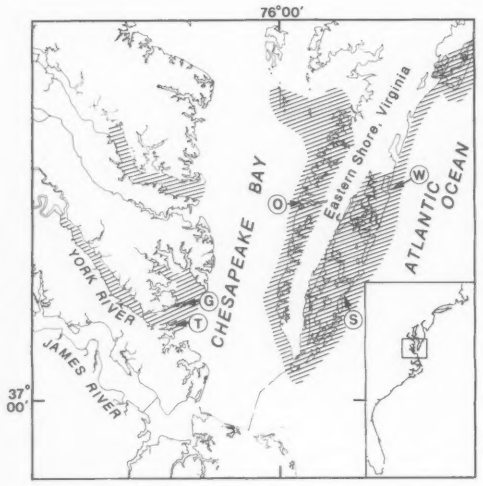


Figure 1

Locations of sampling sites for *Paralichthys dentatus* on Virginia's Eastern Shore and in Chesapeake Bay and its tributaries. Letters indicate sites with regular, fixed station sampling; shading indicates areas in which rivers, creeks, and nearshore locations were sampled during 1986 preliminary investigations and supplemental investigations in July 1987 and June 1988.

Between 1986 and 1989, three different types of 4.9-m semi-balloon otter trawls with 19.1-mm bar mesh in the wings and upper body were used to sample areas 1–11 m in depth. Only bar mesh sizes are noted in this paper. The first unlined trawl, used in 1986 and July 1987, had 6.4-mm mesh in the lower body and codend. We added a 3.2-mm mesh liner to the codend in September to capture the newly settled juveniles. Because ctenophores and jellyfish could clog the mesh, mesh sizes of the unlined trawl were increased to 19.1 mm in the lower body and to 15.9 mm in the codend in August 1987. To compare the sampling efficiency of the lined and unlined trawls, both trawls were towed at each station from September 1987 onward. All trawls were fished with a 4.8-mm link tickler chain to increase catches of flatfish (see Creutzberg et al., 1987).

Two 6.1-mm seines were used to sample shallow (<1 m) habitats. A beach seine (6.4-mm mesh) was used in April and May 1986 and a bag seine (3.2-mm mesh) was used from November 1986 until December 1988. A 3.2-mm link chain was attached to the leadline of both seines to increase catches of flatfish.

Trawling and seining were conducted from April 1986 to August 1989 during daylight hours (Norcross and Hata, 1990). While designing the study from April to August 1986, sampling was conducted at least once in most navigable waters of the Eastern Shore and at the mouth of the York River (Fig. 1). Over the next two years, September 1986–September 1988, samples were collected at fixed stations at five sites (Fig. 1): Wachapreague and Sand Shoal Channels, Occohannock Creek, and Guinea and Tue Marshes (also see Wyanski, 1990). At each site, deep (5–11 m) water stations were located in the middle of channels, whereas shallow (<5 m) water stations were situated along channel margins. All stations had sand or fine-grained substrates. Samples were collected semi-monthly from September 1986 through

August 1987, and at monthly intervals thereafter. During expected periods of peak age-0 summer flounder abundance in 1987 and 1988, additional samples were collected throughout the study area (Fig. 1).

Sampling was reduced spatially and further reduced temporally in 1989. Sampling was eliminated at Occohannock Creek, the site at which the fewest number of summer flounder were captured. Sampling was conducted April through August at the other four sites. Only trawling was continued.

We measured the total length (TL) of each summer flounder and used the length-frequency data to identify age-0 individuals. A birthdate of 1 January (Smith et al., 1981) was used when designating year class, although age-0 summer flounder may have been collected the preceding October through December. For each gear, data from all sampling efforts were pooled by month and by year class and catch per unit of effort (CPUE) was calculated as the mean number of age-0 summer flounder per 15-m seine haul or 5 minutes of trawl sample. To make sample sizes more similar among the treatment groups (year class) in statistical analyses, the 15-month time period over which a year class was sampled was separated into two time intervals: October–June and September–December. July and August data were not included in analyses because of bias produced by the clogging of meshes.

Some data were eliminated from statistical analyses owing to changes in the gear. Only seine data for the 1987 and 1988 year classes were compared because a different seine was used in 1986. Unlined trawl data for the 1986 year class were eliminated because the mesh size was smaller than in subsequent years. Because of nonrandom (fixed) station locations and nonindependent samples, nonparametric statistical tests were used to analyze the CPUE data. For each gear, the Mann-Whitney test or Kruskal-Wallis test was used to compare monthly CPUE values among years (Zar, 1984). If the null hypothesis in the Kruskal-Wallis test was rejected, a multiple comparison test (Dunn, 1964) was used to determine which means were significantly different. If P was <0.05, the results were considered significant.

Results

We were able to identify the age-0 year class for 15 months (October through December of the next year) using length frequencies from all four years of data combined (Fig. 2). Table 1 shows the application of these monthly size-at-age criteria to identify the age-0 specimens in individual years. Sizes ranged from 11 mm to the largest age-0 specimen of 285 mm. Little to no change in mean size was observed from October to May, whereas rapid size changes were apparent from June to September.

Though sampling effort and gear varied among years, age-0 summer flounder were caught within Virginia waters in each year of the study. Over the four years of sampling, age-0 *P. dentatus* were captured each month but not during every month of every year (Table 2). Summer flounder exhibited a prolonged period of recruitment to inshore waters as age-0 specimens were captured in Virginia estuaries from October to May (Table 2, Fig. 2). Newly settled specimens (<20 mm) were collected throughout the fall and winter of 1986–87; however, they were not collected in the fall and winter of 1987–88 and 1988–89. When age-0 specimens first appeared in April of 1988 and 1989, they were already >20 mm.

The highest CPUE values were reported for April through September (Table 2). Comparisons of CPUE

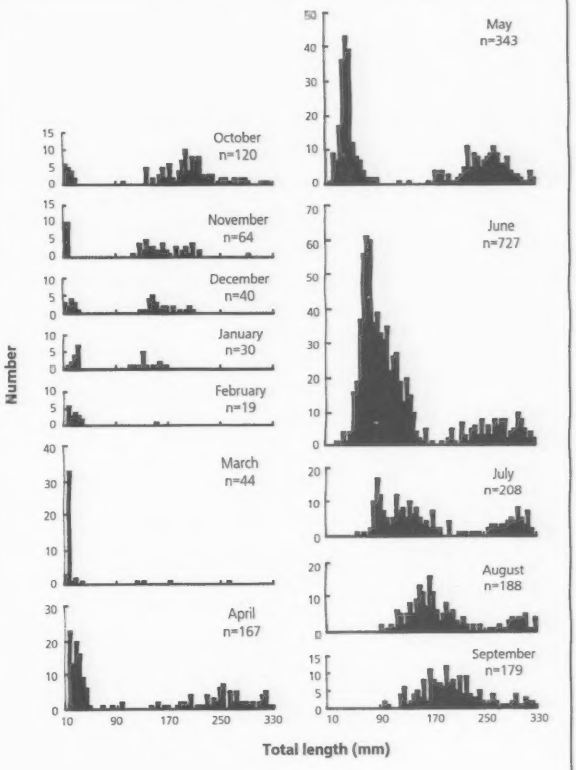


Figure 2

Combined monthly length frequencies of age-0 and age-1 *Paralichthys dentatus* in Virginia captured at all sites shown in Figure 1 from 1986 through 1989.

Table 1

Length ranges (mm) of age-0 summer flounder, *Paralichthys dentatus*, from all sites by year class for 15 months.

	1986 Year class	1987 Year class	1988 Year class	1989 Year class
Oct	—	11–27	—	—
Nov	—	13–19	—	—
Dec	—	14–32	—	—
Jan	—	17–34	—	—
Feb	—	17–38	—	—
Mar	—	14–27	—	—
Apr	26–69	15–48	22–83	36–41
May	22–60	21–80	24–32	17–88
Jun	54–140	27–160	35–160	35–144
Jul	96–190	68–180	86–180	57–160
Aug	30–220	93–240	115–210	90–210
Sep	96–265	147–275	176–222	—
Oct	100–285	170–265	172–245	—
Nov	119–218	—	—	—
Dec	131–185	168–209	—	—

data pooled over the five sampling sites for each of the three gear types showed a general pattern of reduced age-0 summer flounder abundance in Virginia estuaries between 1986 and 1988; there was a slight increase in 1989, based on trawl data (Table 3). The CPUE of the seine and the unlined trawl decreased an order of magnitude per year from 1986 to 1988.

Twice as many summer flounder (101 vs. 54) were captured in seven seine hauls in April and May 1986 as in 527 seine hauls over the next two years (Table 3). For October–June data, CPUE in seine hauls was significantly greater in 1987 than in 1988 (Table 4) as no *P. dentatus* were captured in 1988. Seining, though successful in 1986, did not yield many age-0 flounder in 1987–1988 (Tables 2 and 3), and thus was discontinued.

The unlined trawl data revealed no significant differences in CPUE between years (Table 4). We did not include 1986 unlined trawl data in analyses, but the high CPUE values for this gear type in May and June provided additional evidence that abundance was greater in 1986 compared with 1987–1989.

The lined trawl data for October–June revealed significant differences in CPUE among years (Table

Table 2

Catch per unit of effort (CPUE) of age-0 summer flounder, *Paralichthys dentatus*, by year class for 15 months from all sites. Seine CPUE = number of age-0 flounder/15 m haul; trawl CPUE = number of age-0 flounder/5 min; — = no of sample taken.

	1986 year class (1985–86)			1987 year class (1986–87)			1988 year class (1987–88)			1989 year class (1988–89)		
		Trawl			Trawl			Trawl			Trawl	
Month	Seine	Lined[1]	Unlined[2]	Seine[3]	Lined[1]	Unlined	Seine[3]	Lined[1]	Unlined[4]	Seine[3]	Lined[1]	Unlined[4]
Oct	—	—	—	—	0.03	—	0	0	0	0	0	0
Nov	—	—	—	0.08	0.36	—	0	0	0	0	0	0
Dec	—	—	—	0.24	0.16	—	0	0	0	0	0	0
Jan	—	—	—	0.13	0.14	—	0	0	0	—	—	—
Feb	—	—	—	0.13	0.21	—	0	0	0	—	—	—
Mar	—	—	—	0.29	0.50	—	0	0	0	—	—	—
Apr	16.60[5]	—	—	0.79	0.75	—	0	0.05	0	—	0.06	0
May	9.00[5]	—	13.81	0.33	1.51	—	0	0.13	0	—	1.14	0.29
Jun	—	—	4.08	0.04	3.98	—	0	0.06	0.06	—	3.27	2.00
Jul	—	—	2.01	0.17	3.84	1.38[2]	0	0.14	0.18	—	1.88	2.00
Aug	—	—	3.70	0.08	—	0.96[4]	0	0.26	0.37	—	0.71	1.28
Sep	—	0.87	—	0	0.29	0.65[4]	0	0.22	0.61	—	—	—
Oct	—	0.69	—	0	0.42	1.65[4]	0	0.35	0.43	—	—	—
Nov	0[3]	0.56	—	0	0	1.00[4]	0	0.13	0	—	—	—
Dec	0[3]	0.31	—	0	0	0.17[4]	0	0	0	—	—	—

[1] Semi-balloon otter trawl (3.2-mm mesh liner).
[2] Semi-balloon otter trawl (6.4-mm mesh).
[3] Bag seine (3.2-mm mesh).
[4] Semi-balloon otter trawl (15.9-mm mesh).
[5] Beach seine (6.4-mm mesh).

4); CPUE was higher in 1987 than in 1988. No other differences were detected. For September–December data, there were no significant differences in CPUE among the 1986, 1987, and 1988 year classes (Table 4).

Gear efficiency changed as fish size increased. The unlined trawl with 15.9-mm mesh in the codend produced generally lower CPUE values than the lined trawl during April through June (Table 2). As the age-0 specimens increased in size, the CPUE values for the unlined trawl became higher than those for the lined trawl.

Discussion

The prolonged time of age-0 summer flounder recruitment to the inshore waters of Virginia is more extended than entry times for North Carolina waters where age-0 *P. dentatus* enter estuaries from December through April (Deubler, 1958), January through April (Burke et al., 1991), or February through April (Warlen and Burke, 1990). October through May recruitment to Virginia also agrees with reports of transforming larvae of *P. dentatus* (≤20 mm TL) entering New Jersey inlets from October through May (Able et al., 1990). Age-0 summer flounder were not collected from October through May during all years of our study. They may appear in the fall or winter but often are not evident until April. Similar variation in timing of and size at first collection was reported in New Jersey, where age-0 flounder (<50 mm) were collected in the fall and during May but only occasionally during the winter months (Able et al., 1990). Thus, appearance of summer flounder in Virginia estuaries seems to be more similar to that of New Jersey (fall and late spring) rather than to that seen in North Carolina (winter and early spring). The time of first entrance in New Jersey, Virginia, and North Carolina estuaries corresponds with spawning periods of September–December north, and November–

Table 3

Summary of collection data from all sites by year class for age-0 *Paralichthys dentatus*: number of 15-m seine hauls, number of age-0 flounder captured, seine catch per unit of effort (CPUE) = number of age-0 flounder/haul, number of trawl tows, total minutes tow time for lined and unlined trawls, number age-0 flounder captured, trawl CPUE = number of flounder/5 min tow.

	Year class			
	1986	1987	1988	1989
Seine				
Number of hauls	46	295	232	0
Number of flounder	108	54	0	0
CPUE	1.20	0.18	0.00	—
Lined Trawl				
Number of tows	282	739	320	93
Number of minutes	1410.0	3664.5	1578.5	426.0
Number of flounder	192	670	30	96
CPUE	0.68	0.91	0.10	1.13
Unlined Trawl				
Number of tows	125	206	334	94
Number of minutes	613.8	1015.5	1657.8	467.0
Number of flounder	436	192	33	97
CPUE	3.55	0.94	0.10	1.04

Table 4

Summary of statistical tests used to compare catch per unit of effort (CPUE) for *Paralichthys dentatus* between years for various gear and time intervals. H_0 = the null hypothesis; U = Mann-Whitney (MW) statistic; H = Kruskal-Wallis (KW) statistic; Q = multiple comparison statistic (Dunn, 1964); df = degrees of freedom; * = significant results at 0.05 level of significance.

Gear	Months	H_0	Statistic	P	Test
Seine	Oct–Jun	1987=1988	U=72*	<0.001	MW
Unlined trawl	Oct–Jun	1988=1989	U=34	>0.20	MW
Unlined trawl	Sep–Dec	1987=1988	U=14	0.10<P<0.20	MW
Lined trawl	Oct–Jun	1987=1988=1989	H=10.310* df=2	0.005<P<0.01	KW
		1987=1988	Q=3.22*	0.002<P<0.005	MC (D)
		1987=1989	Q=1.64	0.2<P<0.5	MC (D)
		1988=1989	Q=1.21	P>0.5	MC (D)
Lined trawl	Sep–Dec	1986=1987=1988	H=5.734 df=2	0.05<P<0.10	KW

February south, of Chesapeake Bay as suggested by Smith (1973).

There are several possible explanations for the interannual differences in timing of recruitment to the inshore waters and size at first collection: 1) abundance is so low in some years that age-0 fish are not encountered; 2) newly settled summer flounder are utilizing habitats that were not sampled; and 3) summer flounder juveniles do not enter estuaries at the same time and size in all years.

The first explanation seems plausible for the 1988 year class which apparently had no October 1987–March 1988 recruitment and extremely low numbers in summer (Table 2). However, there also was no October–March recruitment in 1988–89, yet abundance indices in May–August 1989 were comparable to those in 1987, a year with October–May recruitment. We sampled a limited number of fixed sampling sites, thus in years of relatively low abundance, an uneven distribution of the fish would appear as though recruitment did not occur.

Newly settled summer flounder may be utilizing certain habitats which were not sampled because of location or gear accessibility. Habitats, such as eelgrass beds, would be difficult to sample with trawl and seine gear (Able et al., 1990) and therefore the flounder would be unavailable to the gear. Newly recruiting summer flounder are most abundant in marsh creeks in New Jersery (Szedlmayer et al., 1992). In some years of our study, the flounder could have been present in eelgrass beds or marsh creeks that we did not sample. From our data, it would then appear as if winter recruitment had not taken place.

Recruitment of summer flounder juveniles may not be represented by a characteristic place, time, and size of fish. Able et al. (1990) suggested that some juveniles utilize the continental shelf as a nursery and thus enter estuaries at a larger size. This could explain the apparent lack of fall/winter recruitment that we observed in the 1988 and 1989 year classes. Variability in time of recruitment to inshore waters of Virginia observed over the three years of fall/winter sampling in this study is analogous to that in New Jersey waters. Newly recruiting summer flounder were collected in southern New Jersey estuaries from November 1988 through May 1989, but no summer flounder juveniles were collected in the corresponding months of 1987 and 1988 (Szedlmayer et al., 1992).

Variation of year-class strength in fish populations has been a topic of investigation since it was first proposed by Hjort (1914), but fluctuations in year-class strength must be identified before causes of the variation can be investigated. Four years of sampling did not provide sufficient data to define a "normal" level of recruitment; however, it appears that there was relatively poor recruitment of age-0 summer flounder to Virginia waters in 1988 compared with 1986, 1987, and 1989 (Tables 2 and 3), suggesting that there was large interannual recruitment variability. This decrease in year-class strength was verified by catches of age-1 summer flounder in Chesapeake Bay and nearshore coastal waters one year later (Desfosse et al.[1]). The highest CPUE values for the seine and trawls occurred in spring 1986, suggesting that the 1986 year class was possibly the strongest of the four year classes. Given the larger mesh size in the seine and unlined trawl in spring 1986, these high CPUE values are probably underestimates when compared with CPUE values for the seine and lined trawl in 1987–89.

We cannot speculate what effect poor year-class strength of summer flounder will have on the fishery two to four years later because it is not known what percentage of the fishable population is dependent on Virginia nursery areas. If Virginia waters are a primary nursery area, the impact to the fishery could be great. Because our data and those of Desfosse et al.[1] documented poor year classes in 1987–89, the Virginia Marine Resources Commission (VMRC) closed the nearshore (<3 miles) trawl fishery for summer flounder effective 1 July 1989 (Travelstead[2]) as a precautionary measure to protect those year classes.

Estimation of summer flounder juvenile recruitment is biased by small-scale distribution patterns, mesh size, and gear performance under certain conditions. Gear efficiency changes with size of fish. The 3.2- and 6.4-mm mesh seines and trawls used in our study captured smaller specimens in the winter and spring than did the 15.9-mm mesh trawl, but these gear become less efficient with increasing fish size, probably due to increased gear avoidance. Despite similar mesh sizes, the sampling effectiveness of the bag seine decreased more rapidly than did the lined trawl, probably because of the movement of age-0 summer flounder to deeper habitats at 60–80 mm TL (see Wyanski, 1990). No age-0 summer flounder were captured by seine later than August. We agree with Williams and Deubler (1968) that environmental factors, such as current velocity and mechanical clogging of nets, can also have a pronounced effect on sampling success for flounder. We found that gear efficiencies depend on season (e.g. density of jellyfish) and size of flounder.

---

[1] Desfosse, J. C., J. A. Musick, A. D. Estes, and P. Lyons. 1989. Stock identification of summer flounder (*Paralichthys dentatus*), in the southern Mid-Atlantic Bight. Virginia Inst. Mar. Sci., Gloucester Point, VA 23062. Ann. Prog. Rep. WB-86-01-03.

[2] Travelstead, J. VMRC, Newport News, Virginia 23607. Personal commun., June 1989.

To develop an index to monitor interannual variation in year-class strength of summer flounder, we suggest sampling in Virginia estuaries during April, May, and June with a small mesh (e.g. 3.2 mm) lined beam trawl. Beam trawls (Kuipers, 1975; Kuipers et al., 1992) have been found to be more effective at capturing flatfishes than have otter trawls (Gunderson and Ellis, 1986) which were used in this study. We recommend using a beam trawl with tickler chains to increase catch, particularly on sand or fine-grained sediment. Diver observations and catch comparisons of flatfishes by beam and otter trawls in Alaskan waters (Norcross, unpubl. data) support this recommendation.

Though summer flounder can be captured through October (Fig. 2), the fish are larger but fewer from July to October. This pattern of increasing densities during the period of settlement, followed by a continuous decrease has also been observed in plaice (*Pleuronectes platessa*) in the North Sea (Veer et al., 1990). Thus we recommend sampling during the period of increasing densities, because later in the season low numbers of captured individuals reduce the sensitivity of the catch data to reflect year-class strength.

Data presented here support the hypothesis of Poole (1966) that Virginia waters are a nursery ground for summer flounder. Variation in CPUE during the four years of our study makes it difficult to conclude that this area is a "primary" nursery during all years.

In addition to Virginia, summer flounder use areas in New Jersey (Szedlmayer et al., 1992), Delaware (Malloy and Targett, 1991) and North Carolina (Burke et al., 1991) as nursery grounds. The same sample gear and strategy need to be used throughout the range of summer flounder (New Jersey to North Carolina) to compare the relative importance of specific locations as nursery areas. A multi-year study combined with sampling over a finer spatial scale would allow interannual variation in primary nursery locations to be determined.

Acknowledgments

We thank S. Smith, D. Seaver, D. Estes, D. Hata, S. Bradberry, D. Bodolus, L. Marshall, C. Tabit, the crews of the RV *Captain John Smith* and NOAA Ship *Ferrel* for their field assistance, and M. Castagna for logistical support. Funding for this project was awarded by the National Marine Fisheries Service, Northeast Fisheries Science Center (Contract No. NA85-EAH-00026), by the National Sea Grant College Program (Sub-contract No. 5-29532), and by the Council on the Environment (State of Virginia). Additional support for data analysis was supplied by the Institute of Marine Science, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks.

Literature cited

Able, K. W., R. E. Matheson, W. W. Morse, M. P. Fahay, and G. Shepard.
1990. Patterns of summer flounder *Paralichthys dentatus* early life history in the Mid-Atlantic Bight and New Jersey estuaries. Fish. Bull. 88:1–12.

Burke, J. S., J. M. Miller, and D. E. Hoss.
1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Neth. J. Sea Res. 27:393–405.

Creutzberg, F., G. C. A. Duineveld, and G. J. van Noort.
1987. The effect of different numbers of tickler chains on beam-trawl catches. J. Cons. int. Explor. Mer 43:159–168.

Deubler, E. E.
1958. A comparative study of the postlarvae of three flounders (*Paralichthys*) in North Carolina. Copeia 1958:112–116.

Dunn, O. J.
1964. Multiple contrasts using rank sums. Technometrics 6:241–252.

Gunderson, D. R., and I. E. Ellis.
1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish. Res. 4:35–41.

Gutherz, E. J.
1967. Field guide to the flatfishes of the family Bothidae in the western North Atlantic. U.S. Fish Wildl. Serv., Circ. 263, 47 p.

Hjort, J.
1914. Fluctuations in the great fisheries of northern Europe. Rapp. P.-v. Reun. Cons. int. Explor. Mer 20:1–13.

Kuipers, B. R.
1975. On the efficiency of a two metre beam trawl in juvenile plaice (*Pleuronectes platessa*). Neth. J. Sea Res. 9:69–85.

Kuipers, B. R., B. MacCurrin, J. M. Miller, H. W. van der Veer, and J. IJ. Witte.
1992. Small trawls in juvenile flatfish research: their development and efficiency. Neth. J. Sea Res. 29:109–117.

Malloy, K. D., and T. E. Targett.
1991. Feeding, growth and survival of juvenile summer flounder *Paralichthys dentatus*: experimental analysis of the effects of temperature and salinity. Mar. Ecol. Prog. Ser. 72:213–223.

Miller, J. M., J. P. Reed, and L. J. Pietrafesa.
1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. *In* J. D. McCleave, G. P.

Arnold, J. J. Dodson, and W. H. Neill (eds.), Mechanisms of migration in fishes, p. 209–225. Plenum Publ. Corp.

Norcross, B. L., and D. Hata.
1990. Seasonal composition of finfish in waters behind the Virginia barrier islands. Va. J. Sci. 41:441–461.

Orth, R. J., and K. L. Heck Jr.
1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bayfishes. Estuaries 3:278–288.

Poole, J. C.
1966. A review of research concerning summer flounder and needs for further study. N.Y. Fish Game J. 13:226–231.

Powell, A. B., and F. J. Schwartz.
1977. Distribution of paralichthid flounders (Bothidae: *Paralichthys*) in North Carolina estuaries. Chesapeake Sci. 18:334–339.

Richards, C. E., and M. Castagna.
1970. Marine fishes of Virginia's eastern shore (inlet and marsh, seaside waters). Chesapeake Sci. 11:235–248.

Scarlett, P. G.
1981. Fishery management plan for the summer flounder (*Paralichthys dentatus*) fishery. Atl. States Mar. Fish. Comm., Fish. Manage. Rep. 3, 80 p.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Smith, W. G.
1973. The distribution of summer flounder, *Paralichthys dentatus*, eggs and larvae on the continental shelf between Cape Cod and Cape Lookout, 1965–66. Fish. Bull. 71:527–548.

Smith, R. W., L. M. Dery, P. G. Scarlett, and A. Jearld Jr.
1981. Proceedings of the summer flounder (*Paralichthys dentatus*) age and growth workshop, 20–21 May 1980, Northeast Fisheries Center, Woods Hole, Massachusetts. NOAA Tech. Memo., NMFS-F/NEC-11, 30 p.

Szedlmayer, S. T., K. W. Able, and R. A. Roundtree.
1992. Growth and temperature-induced mortality of young-of-the-year summer flounder (*Paralichthys dentatus*) in southern New Jersey. Copeia 1992:120–128.

Veer, H. W. van der, L. Pihl, and M. J. Bergman.
1990. Recruitment mechanisms in North Sea plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 64:1–12.

Warlen, S. M., and J. S. Burke.
1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–461.

Weinstein, M. P., and H. A. Brooks.
1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12:15–27.

Wilk, S. J., W. G. Smith, D. E. Ralph, and J. Sibunka.
1980. Population structure of summer flounder between New York and Florida based on linear discriminant analysis. Trans. Am. Fish. Soc. 109:265–271.

Williams, A. B., and E. E. Deubler Jr.
1968. A ten year study of macroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27–41.

Wyanski, D. M.
1990. Patterns of habitat utilization in 0-age summer flounder (*Paralichthys dentatus*). M.A. thesis, College of William and Mary, 54 p.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 718 p.

Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* (Decapoda: Aristeidae) population in the western Mediterranean

Francisco Sardà
Joan E. Cartes
Walter Norbis*
Instituto de Ciencias del Mar (CSIC), Paseo Nacional s/n
08039 Barcelona, Spain

Abstract.—The spatio-temporal structure of a population of the deep-water shrimp *Aristeus antennatus* on the fishing grounds off Barcelona, Spain, in the western Mediterranean Sea was studied, and the relationship between fluctuations in catch of this species and spatio-temporal changes in the size and sex composition of shoals is described. Fluctuations were monitored by using a sample design based on fixed seasonal sampling of three different habitats (upper submarine canyon, middle slope, and lower slope). The results explain changes in fishing fleet and fishing location. The stock appears to remain constant at approximately optimum levels of exploitation because part of it is unexploited below 1,000 m.

Factorial correspondence analysis indicated a generally strong influence of depth on the abundance of deep-water shrimp, explaining 63.14% of the variance. However, the influence of seasonality was stronger when only samples taken at depths shallower than 1,000 m (75.22%) were considered. Females contributed most to the catches on the upper and middle slope throughout the year, and catches of females were strongly related to seasonality ($P<0.05$). The combined interaction of depth and seasonality on the abundance of males was significant ($P<0.05$). Juveniles were present in the catches from autumn to spring, and the combined effect of depth and seasonality on the abundance of juveniles was also significant ($P<0.05$). The role of the regional submarine canyon as a zone of higher energy and biomass in the recruitment of this species is discussed, and the importance of spatio-temporal factors linked to the life cycle of deep-water shrimps is highlighted. The results demonstrate that comprehensive ecological studies of exploited species are essential to proper fisheries management.

As fishing activity has expanded into deeper waters, deep-water shrimps (Dendrobranchiata and Caridea) have become an important resource in different parts of the world, e.g. Australia (King, 1981; King and Butler, 1985) northern Europe (Anon., 1992), and the Pacific (Gooding, 1984) and Indian (Jones, 1969) oceans. In the Mediterranean Sea in particular, these shrimps are the target of a traditional fishery (Relini and Orsi Relini, 1987; Tobar and Sardà, 1987; Campillo et al., 1990; Demestre, 1990; Demestre and Lleonart, 1993). In addition, deep-water shrimps, particularly aristeid species (Dendrobranchiata, Penaeoidea: *Aristeus antennatus* Risso, 1816), play an important ecological role in Mediterranean deep-sea communities at depths below 400 m (Pérès, 1985; Abelló et al., 1988; Abelló and Valladares, 1988; Cartes and Sardà, 1993). Population structure, biological cycles, life history, and spawning strategies of deep-water shrimps differ from those of littoral species (García and Le Reste, 1987) and are poorly understood. The life history of deep-water penaeoidean species is not dependent upon lagoonal or littoral systems, and growth in such species tends to be slower than that in littoral penaeid species (García and Le Reste, 1987; Demestre, 1990). The presence and abundance of such species are linked to the topography of the continental slope and submarine canyons. However, their behavioral patterns are complex and not well understood (Tobar and Sardà, 1987; Cartes et al., 1993).

Pandalus borealis (Anon., 1992) (Pandalidae, Caridea) is the most extensively studied shrimp species from a fisheries perspective. This species exhibits major differences with respect to species of other genera inhabiting subtropical deep-sea regions, such as *Aristeus*, *Aristaeomorpha*, *Parapandalus*, and *Plesionika*; it is protandrously hermaphroditic and distributed in shallower waters. Migratory patterns, short and medium-term fluctuations in abundance, aggregating behavior, recruitment, and larval and postlarval dis-

Manuscript accepted 30 November 1993.
Fishery Bulletin 92:599–607 (1994).

* Permanent address: INAPE, Constituyente, 1497
CP 11200, Montevideo, Uruguay

tribution patterns are to a large extent still unknown in deep-water species of the latter genera.

Moreover, recently published data on the distribution and abundance of deep-water shrimps in the western Mediterranean (*Aristeus antennatus*, *Acanthephyra eximia*, *Nematocarcinus exilis*) indicate relatively high biomass levels for these species at depths down to 2,200 m (Abelló and Valladares, 1988; Cartes and Sardà, 1992, 1993; Sardà and Cartes, 1993a). Fishing pressure in shallow waters has resulted in a shift of effort to deeper regions, making the study of deepwater species extremely important, while exploitation of these resources is still low (King, 1981; Demestre, 1990; Demestre and Lleonart, 1993). Growth, reproductive biology and morphometry of *Aristeus antennatus* in particular has been studied by several authors (e.g. Bas, 1965; Relini Orsi and Relini, 1979; Arrobas and Ribeiro-Cascalho, 1987; Sardà and Demestre, 1987; Demestre and Fortuño, 1992; Sardà et al., in press). In contrast, the only available information on population structure (sex-ratio, size distribution, proportion of juveniles) and spatio-temporal migrations has been compiled from commercial fisheries data (Relini and Orsi Relini, 1987; Tobar and Sardà, 1987, 1992).

The objective of the present study is to examine the relationship between fisheries exploitation and the distribution and spatio-temporal structure of a population of *A. antennatus* in the three different habitats occupied by this species: submarine canyons on the upper slope, the middle slope, and lower slope. The study attempts to integrate our basic knowledge of the biology and population structure of this species with the pattern of fishing activity in the region. We provide a basis for interpreting catch fluctuations observed during the year and for managing this fishery consistent with the general ecology of the species.

Materials and methods

Sampling was designed to survey spatio-temporal features in two different habitats (one station in each) where commercial catches of *A. antennatus* were common: the submarine canyon known as "La Merenguera" located on the upper slope (US) at a depth of approximately 450 m (41°07'75"N, 02°04'43"E) and the area known as the "Abisinia" fishing grounds on the middle slope (MS) at a depth of 600–650 m (41°06'34"N, 02°12'05"E). A third station was located on the upper portion of the lower slope (LS) at a depth of about 1,200 m (41°54'63"N, 02°06'90"E), where no fishing activity takes place (Fig. 1). Habitat nomenclature follows Pérès (1985). Three replicate tows were carried out within a period of less than 12 hours at each sampling station in summer, autumn, winter, and spring (Table 1). The trawl gear was a "Maireta system" (Spanish patent: 9200614, Inst. Ciencias del Mar [CSIC], consisting of a semi-balloon otter trawl with square panels and wings and a 25-m headline. The gear was towed by a single warp line attached to a V-shaped backstrop, which was in turn connected to two 450-kg iron doors. The horizontal gear opening (the wing-end spread of 14 m) was measured by using a SCANMAR system. Codend stretch mesh size was 2 mm (Sardà et al., 1993). Trawls were conducted by the Research Ship *García del Cid*.

Towing speed was 2.5 knots for all trawls. Starting and ending positions of each tow were recorded by using a GPS system. Specimens of *A. antennatus* were weighed and sexed (M=males; F=females), and short carapace length (CL) in mm was measured (rear edge of ocular orbit to rear edge of carapace). Male and female individuals smaller than 23 mm CL were classified as juveniles (J) (Sardà and Demestre, 1987; Demestre, 1990). Smaller individuals (CL <15 mm) were uncommon in the samples; such

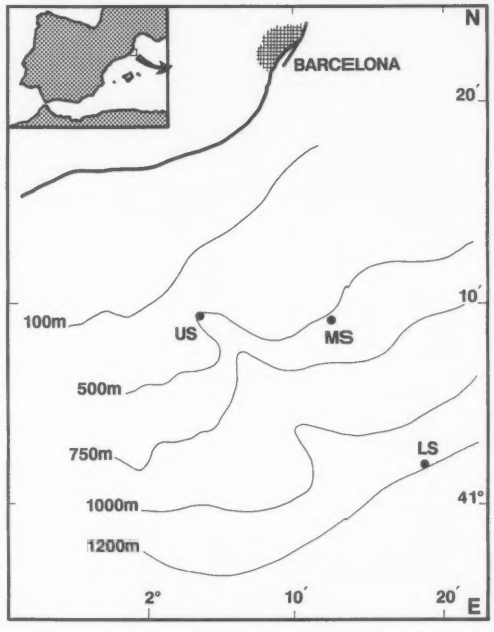


Figure 1

Map of the study area showing the location of sampling stations. US=upper slope; MS=middle slope; LS=lower slope (see text for explanation).

individuals were considered to represent the early juvenile stages (L) and were analyzed separately to obtain information on the earliest stages of recruitment.

Spatio-temporal changes in population structure were analyzed by using factorial correspondence analysis (FCA) (Benzecri, 1980; Greenacre, 1984). Data were logarithmically transformed and a data matrix was constructed by using the three habitats sampled and the following variables: number of males (M), number of females (F), number of juveniles (J), number of smaller juveniles (L), and total number. Because the LS below 1,000 m is a stable habitat that, unlike the US and MS, is less affected by seasonal factors (Hopkins, 1984; Tyler, 1988; Gage and Tyler, 1991) and is not exploited by the fishery (Demestre, 1986; Sardà and Martín, 1986), the analysis was repeated excluding samples taken on the LS (Table 2).

Multifactorial nonparametric analysis of variance (Zar, 1984) was used to calculate differences between variable and habitat combinations in each season (spring, summer, fall, and winter). The Mood nonparametric median test (Conover, 1980) was also used to determine differences in total number of individuals by habitat.

Table 1

Sample list and specific haul data for collections of rose shrimp, *Aristeus antennatus*. P=spring; W= winter; A=autumn, and S=summer. US=upper slope; MS=middle slope, and LS=lower slope.

Ref. code	Season	Habitat	Date	Haul time (h)	Mean depth (m)
R1/1	P	MS	04/23/91	1.00	570
R1/2	P	MS	04/23/91	1.50	600
R1/3	P	MS	04/23/91	1.67	692
R1/4	P	US	04/23/91	1.00	455
R1/5	P	US	04/23/91	1.00	459
R1/6	P	US	04/23/91	1.00	390
R1/7	P	LS	04/25/91	1.00	1160
R1/8	P	LS	04/25/91	1.00	1210
R1/9	P	LS	04/25/91	1.00	1230
R2/7	A	MS	12/09/91	1.00	625
R2/8	A	MS	12/09/91	1.00	613
R2/9	A	MS	12/09/91	2.00	562
R2/1	A	US	12/08/91	0.42	433
R2/2	A	US	12/08/91	0.50	455
R2/3	A	US	12/08/91	0.50	504
R2/4	A	LS	12/08/91	1.00	1265
R2/5	A	LS	12/09/91	1.00	1274
R2/6	A	LS	12/09/91	0.50	1252
R3/1	W	MS	03/12/92	0.83	565
R3/2	W	MS	03/12/92	0.75	545
R3/3	W	MS	03/12/92	0.75	545
R3/4	W	US	03/12/92	0.50	355
R3/5	W	US	03/12/92	0.50	447
R3/6	W	US	03/12/92	0.50	508
R3/7	W	LS	03/13/92	1.00	1235
R3/8	W	LS	03/13/92	1.00	1275
R3/9	W	LS	03/13/92	1.00	1210
R4/1	S	MS	07/26/92	1.00	605
R4/2	S	MS	07/26/92	1.00	611
R4/3	S	MS	07/26/92	1.00	616
R4/4	S	US	07/26/92	0.50	426
R4/5	S	US	07/26/92	0.42	400
R4/6	S	US	07/26/92	0.50	440
R4/7	S	LS	07/27/92	1.00	1260
R4/8	S	LS	07/27/92	1.00	1286
R4/9	S	LS	07/27/92	1.00	1272

Results

The first two inertial axes of the correspondence analysis explained 63.14% and 26.84% of the variance in abundance of shrimp, respectively (Fig. 2). Along the first axis, LS samples were associated with a higher proportion of males and early juvenile stages (L), which did not exhibit any marked seasonal pattern in the deepest region. However, the samples collected in summer on both the US and MS were mainly females and were located in the region opposite the LS samples (Fig. 2). In summary, the first axis was mainly related to depth and juveniles predominated in the US and MS samples collected in spring, autumn, and winter.

The results of the analysis, excluding samples taken on the LS (Fig. 3), yielded a cluster of data points for spring samples associated with the presence of juveniles (recruits); in contrast, data points for summer samples were again associated with adult females. Autumn and winter samples were less clearly discriminated but shifted to the right from the origin and were associated with males. This may be interpreted as a seasonal effect that alters the population structure and is discriminated by the first axis, which explained 75.22% of the total variance (Fig. 3A). The distribution of juveniles appeared to be linked to the topography of the submarine canyons (black points in Fig. 3B), mainly during winter and spring, while the proportion of males rose on the middle slope out to the canyon in autumn and winter (open symbols, Fig. 3B). Juveniles and early juvenile stages (L) were caught in the deepest region sampled (Table 2 and Fig. 2). In summer females were distributed extensively on both the MS and the US. In this second analysis the first axis may be related to seasonality. The second axis (20.27%) probably represents a depth-related component, because the samples from the MS were taken at slightly greater depths (600–650 m) than those taken from the US (400–500 m).

Table 2

Basic data matrix in number of individuals per sample of *Aristeus antennatus:* M=males; F=females; J=juveniles (CL<23 mm); L=early juvenile stages (CL<15 mm); *n*=total number; US=upper slope; MS=middle slope; LS=lower slope. P=spring; A=autumn; W=winter and S=summer, (—)=no data.

		US			MS			LS		
Replicates		1	2	3	1	2	3	1	2	3
	M	74	15	48	153	51	31	—	39	19
	F	359	113	298	178	314	132	—	21	15
P	J	241	60	166	198	86	73	—	40	24
	L	0	0	0	0	0	0	—	0	0
	n	433	128	346	331	265	163	—	60	34
	M	40	82	44	7	5	4	11	24	36
	F	160	378	166	5	8	17	14	11	14
A	J	112	160	94	8	5	4	19	29	42
	L	0	0	0	0	0	0	1	0	0
	n	200	460	160	12	13	21	25	35	50
	M	0	12	6	130	11	24	4	26	25
	F	0	62	42	212	30	107	3	15	12
W	J	0	32	32	102	11	20	4	23	22
	L	0	0	0	0	0	0	0	3	3
	n	0	74	48	342	41	131	7	41	37
	M	18	12	0	0	4	0	63	51	353
	F	820	144	166	53	104	196	45	14	120
S	J	52	30	4	41	5	5	65	40	285
	L	0	0	0	0	0	0	4	2	6
	n	838	156	166	53	108	196	108	65	473

Seasonal groupings of samples revealed significant differences in the analysis of variance (Table 3). When the deepest station (LS) was included in the analysis, the total number of individuals were significantly different with depth ($P<0.05$). This variation with depth can be explained by the fact that, on average, fewer individuals were collected at the station on the LS ($P<0.01$) (Fig. 4).

Differences in the number of females were also significantly related to depth ($P<0.05$); females were more abundant at shallower stations on the MS and US. Males collected from the three habitats exhibited significant differences for interaction between depth and seasonality ($P<0.05$) (Table 3), which resulted from the higher percentage of males on the LS all year and on the MS in autumn and winter.

When the deepest samples (LS) were excluded, differences between the number of males and the total number of individuals were significant between seasons ($P<0.05$) and for the interaction between depth and season ($P<0.05$).

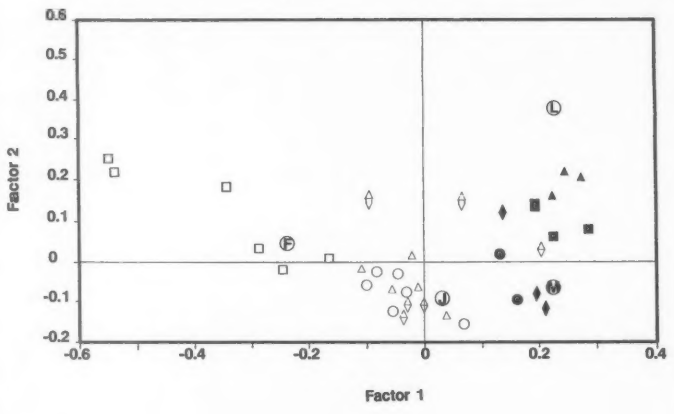


Figure 2

Plots of scores on the first two correspondence axes for the entire set of samples of rose shrimp, *Aristeus antennatus*. F=females; M=males; J=juveniles; L=early juvenile stages; circle=spring; square=summer; triangle=autumn; diamond=winter.

Discussion

The distribution of *A. antennatus* extended to a depth of more than 2,200 m. The population structure in

the deeper region between 1,000 and 2,200 m consisted of a higher proportion of juveniles and males (Cartes and Sardà, 1992; Sardà and Cartes, 1993b; Cartes, in press). This contrasts with the high proportion of females collected at depths of less than 1,000 m.

The present results support the hypothesis that two different populations of *A. antennatus* persist in the western Mediterranean. One population is unexploited and stable throughout the year at depths below 1,000 m and is characterized by lower densities and higher percentages of males and juveniles. The other population is commercially exploited and variable over the year at shallower depths between 400 and 1,000 m. It is characterized by high abundance and by seasonal variations in total number, sex ratio, and depth distribution.

The *A. antennatus* stock, though subjected to considerable fishing pressure, has remained at near optimum equilibrium levels (Demestre and Lleonart, 1993). Sardà (1993) and Sardà and Cartes (1993a) attributed this equilibrium to the presence of unexploited biomass at depths below 1,000 m, which annually renews the exploited portion of the stock.

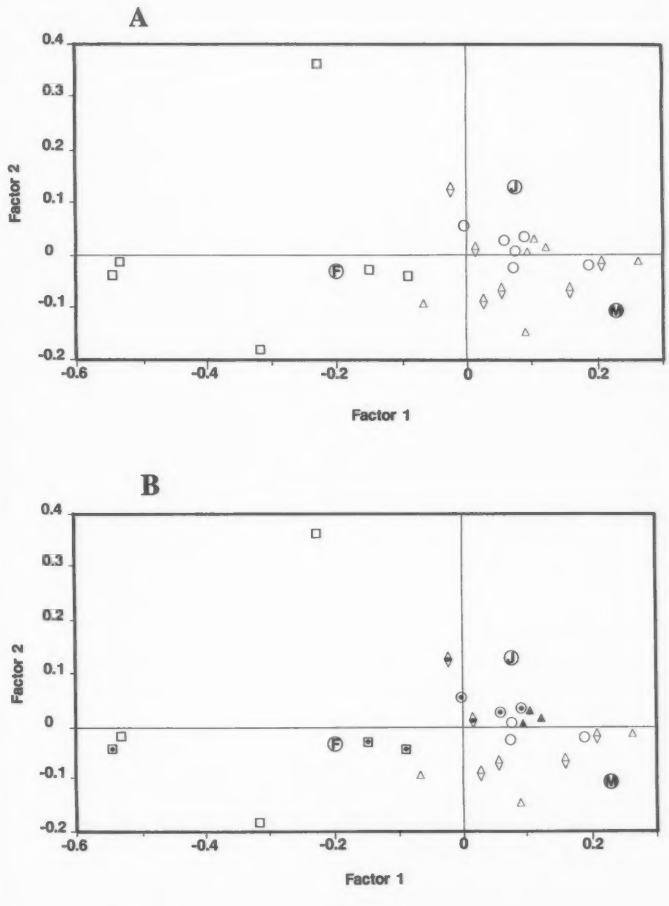


Figure 3

Plots of scores on the first two correspondence axes (**A**) and (**B**) for the entire set of samples of rose shrimp, *Aristeus antennatus* collected on the upper slope (US) and middle slope (MS) only. F=females; M=males; J=juveniles; circle=spring; square=summer; triangle=autumn; diamond=winter. Black points (•) represent canyon samples on upper slope (US).

Though sampling was localized and did not cover extensive areas of each habitat, the samples from the US and MS nonetheless reflected specific spatio-temporal patterns in population structure: females completely dominated the population all year, forming aggregations on the MS in spring and summer. Earlier studies on fishing patterns during the year (Figure 5A, revised after Tobar and Sardà, 1987) have referred to this population migration pattern. Changes in the coefficient of variation of catch rate illustrated in Figure 5B reflect a scattering of the shoals in spring and summer (from April to August) and a more highly aggregated stock structure in autumn and winter. Figure 6 summarizes our conclusions regarding the distribution and movement of *A. antennatus*.

The increase in number of females on the MS in spring and summer coincides with the period of gonadal ripening and fertilization (Relini Orsi and Relini, 1979; Arrobas and Ribeiro-Cascalho, 1987; Sardà and Demestre, 1987; Demestre and Fortuño, 1992) and shortening of the male rostrum (Sardà and Demestre, 1989). These authors also reported that shoals disperse after spawning, which occurs mainly from June to September. This might suggest a specific mating area in the MS. After September, shrimps spread out over the slope and submarine canyons, leading to a decrease in density and increase in the proportion of males on the slope. Processes linked to the transfer of energy through the slope and submarine canyon systems (Reyss, 1971, 1973; or Rowe, 1971;

Koslow and Ota, 1981; Houston and Haedrich, 1984), and feeding habits (Cartes and Sardà, 1989; Cartes, 1991) may also be related to distribution of *A. antennatus*. Ghidalia and Bourgois (1961) and Bombace (1975) associated certain shrimp species with water masses that were of a characteristic septentrional type, with a low temperature of 12.8°C and high salinity (38.1–38.8 ppt). However, it has not been possible to confirm these hydrographic hypotheses for *A. antennatus*, because the study by Ghidalia and Bourgois (1961) reported few catch data of this species. No other studies on related species have established more specific hypotheses.

The growth, abundance, parent stock biomass, and recruitment of commercial species are important when calculating parameters directly related to their population dynamics and exploitation (Caddy and Sharp, 1988; Sardà, 1993). Size-frequency data for *A. antennatus* caught by commercial fishing vessels (Demestre, 1990; Fig. 7) do not show progressions in monthly length-frequency modes. Apparent "negative growth rates" between different months suggest that vessels were following a moving stock and that catches were taken at the most commercially profitable locations. Procedures for analyzing this type of stock have been considered by Jones (1984), Caddy (1982, 1987), and Caddy and García (1986) from fishery catches. Procedures for treating migratory stocks have been considered primarily by Sousa (1988) in the fish *Decapterus russelli*. Bias in size frequencies due to migratory effects in *D. russelli* is similar to

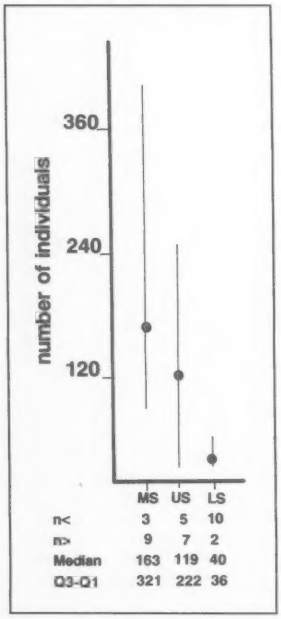


Figure 4

Mean number of individuals of rose shrimp, *Aristeus antennatus*, showing 95% confidence intervals (χ^2=8.67; P< 0.01): 'n<'=number of samples below median; 'n>'=number of samples above median; Q3-Q1= difference between maximum and minimum value. US=upper slope; MS=middle slope; LS=lower slope.

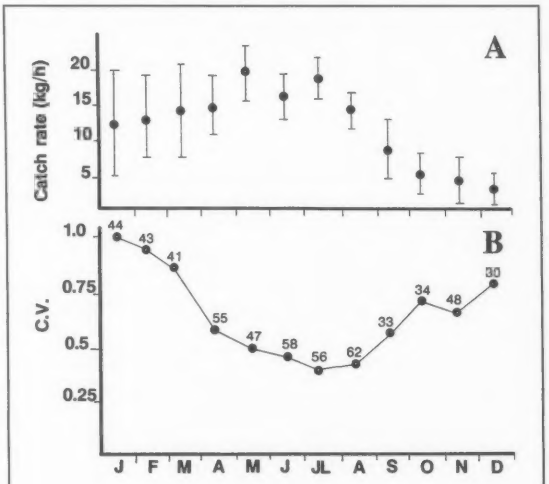


Figure 5

Monthly catch rates (**A**) and coefficient of variation (**B**) based on daily catches of rose shrimp, *A. antennatus*, taken by a vessel during 1984, 1985, and 1986 (redrawn after Tobar and Sardà, 1987). Numbers are total number of samples by month for all three years combined.

Table 3

Results of applying multifactorial nonparametric analysis of variance to the basic data matrix presented in Table 2 for collections of rose shrimp, *Aristeus antennatus*, with and without lower slope (LS) data. M = males; F = females; J=juveniles, n=total number; (+)=significant difference (P<0.05); (—)=nonsignificant difference.

	With LS data				Without LS data			
	M	F	J	n	M	F	J	n
Seasonality	+	—	—	+	—	—	—	—
Depth	—	—	—	—	—	+	—	+
Interaction	+	—	—	+	+	—	+	—

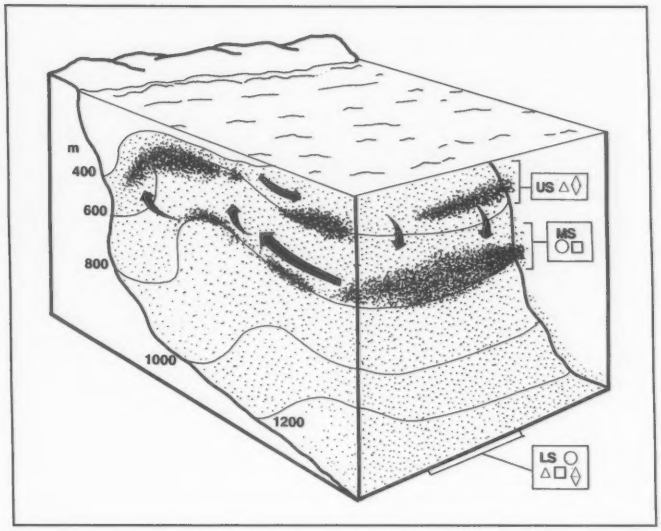


Figure 6

Conceptual model of the spatio-temporal dynamics of *Aristeus antennatus* in the study area (see text for more more details). MS=middle slope; US=upper slope, and LS=lower slope; circle= spring; square=summer; triangle=autumn; diamond=winter.

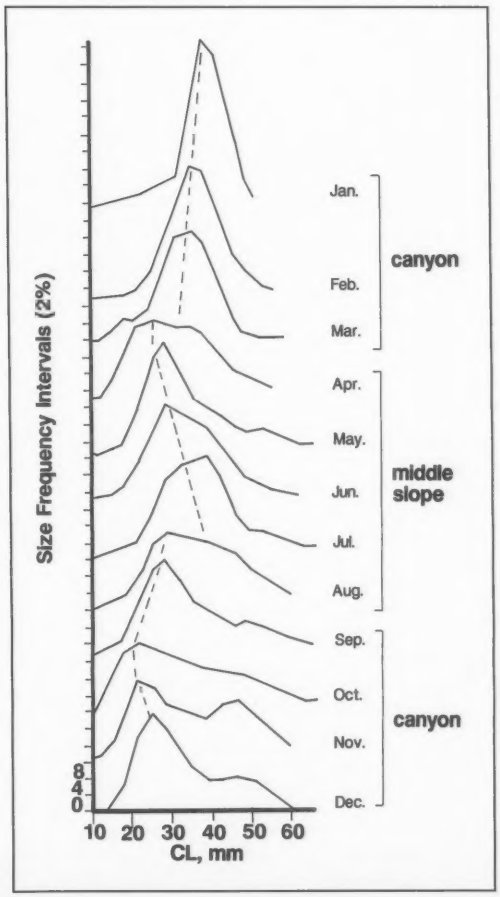


Figure 7

Monthly size frequencies for rose shrimp, *Aristeus antennatus* (carapace length) taken in commercial catches from the upper slope (US) and middle slope (MS) (data from Demestre, 1990).

that observed for *A. antennatus*. Size-frequency modes were evident in spring and summer but did not progress in autumn and winter (Fig. 6). Sparre et al. (1989) advised using the annual-return matched sample method to estimate growth parameters in such cases. Failing to take these aspects into account when considering a population exploited by a given fleet in a given area may lead to errors in calculating biological parameters and, consequently, in decision-making for fishery management.

Acknowledgments

We thank J. B. Company for his assistance in collecting the samples and G. Fuster and J. M. Anguita for our technical assistance. We also wish to express their appreciation to all the team members who participated in the MAR90/757 project, funded by the Spanish Ministry of Education and Science (CICYT). W. Norbis was supported by a doctoral grant from the Agencia Española de Cooperación Internacional del Ministerio de Asuntos Exteriores. R. Sacks prepared the English translation.

Literature cited

Anonymous.
1992. Working group on *Nephrops* and *Pandalus* stocks. ICES. CM. 1992/Assess. 8:1–275.

Abelló, P., and F. J. Valladares.
1988. Bathyal decapod crustaceans of the Catalan Sea (northwestern Mediterranean). Mésogée 48:47–102.

Abelló, P., F. J. Valladares, and A. Castellón.
1988. Analysis of the structure of decapod crustacean assemblages off Catalan coast (North-West Mediterranean). Mar. Biol. 98:39–49.

Arrobas, I., and A. Ribeiro-Cascalho.
1987. On the biology and fishery of *Aristeus antennatus* (Risso, 1816) in the South Portuguese coast. Inv. Pesq. 51 suppl. 1:233–244.

Bas, C.
1965. La gamba rosada (*Aristeus antennatus*). Publicaciones Técnicas de la Junta de Estudios de Pesca 5:143–155.

Benzecri, J. P.
1980. L' analyse des données. 2: L'analyse des correspondences. Ed. Dunod, Paris, 632 p.

Bombace, G.
1975. Considerazione sulla distribuzione delle populazione di livello batiale con particulare referimento a quelle bentonectoniche. Pubbl. Zool. Napoli, 39, suppl. 1:7–21.

Caddy, J. F.
1982. Some considerations relevant to the definition of shared stocks and their allocation between adjacent economic zones. FAO Fish. Circ. 749:1–44.
1987. Size-frequency analysis for crustacea: moult increment and frequency models for stock assessment. Kuwait Bull. Mar. Sci. 9:43–61.

Caddy, J. F., and S. García.
1986. Fisheries thematic mapping—a prerequisite for intelligent management and development of fisheries. Oceanogr. Trop. 21(1):31–52.

Caddy, J. F., and G. D. Sharp.
1988. Un marco ecológico para la investigación pesquera. FAO. Doc. Téc. Pesca 283:1–155.

Campillo, A., P. Y. Dremiere, B. Liorzou, and J. L. Bigot.
1990. Observations sur deux crustacés profonds du Golfe du Lyon: *Aristeus antennatus* (R.) et *Nephrops norvegicus* (L.). FAO. Rap. sur les Pêches 447:298–313.

Cartes, J. E.
1991. Analisis de las comunicdades y estructura trofica de crustaceos decapodos. Ph.D. diss., Universidad de Barcelona, 627 p.
In press. Influence of depth and seasonality on the diet of the deep-water aristeid *Aristeus antennatus* along the slope (between 400–2,300 m) in the Catalan Sea (western Mediterranean). Mar. Biol.

Cartes, J. E., and F. Sardà.
1989. Feeding ecology of the deep-water aristeid crustacean *Aristeus antennatus*. Mar. Ecol. Prog. Ser. 54:229–238.
1992. Abundance and diversity of decapod crustaceans in the deep Catalan Sea (western Mediterranean). J. Nat. Hist. U.K. 26:1305–1323.
1993. Zonation of the deep-sea decapod fauna in the Catalan Sea (western Mediterranean). Mar. Ecol. Prog. Ser. 94:27–34.

Cartes, J. E., F. Sardà, J. B. Company, and J. Lleonart.
1993. Day-light migrations by deep-sea decapod crustaceans in experimental sampling in the western Mediterranean. J. exp. Mar. Biol. Ecol. 171:63–73.

Conover, W. J.
1980. Practical non-parametric statistics, 2nd ed. John Wiley & Sons, New York, 493 p.

Demestre, M.
1986. Les diferents comunitats naturals de la Méditerranée. *In* J. Lleonart (ed.), L'Oceanografía, recursos pesquers de la mar Catalana. Quad. Ecol. Aplicada. Diputació de Barcelona (9):9–41.
1990. Biología pesquera de la gamba *Aristeus antennatus* (Risso, 1816) en el mar Catalán. Ph.D. diss., Univ. Barcelona, 443 p.

Demestre, M., and J. M. Fortuño.
1992. Reproduction of the deep-water shrimp *Aristeus antennatus* (Decapoda: Dendrobranchiata). Mar. Ecol. Prog. Ser. 84:41–51.

Demestre, M., and J. Lleonart.
1993. The population dynamics of *Aristeus antennatus* (Decapoda: Dendrobranchiata) in the northwestern Mediterranean. Sci. Mar. 57(2–3):183–189.

Gage, J. D., and P. A. Tyler.
1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge Univ. Press, London, 503 p.

García, S., and L. Le Reste.
1987. Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO Doc. Tec. Pesca 203:1–180.

Ghidalia, W., and F. Bourgois.
1961. Influence de la témperature et de l'éclairement sur la distribution des crevettes des moyennes et grandes profondeurs. Stud. Rev. Gen. Fish. Count. Medit., FAO 16:1–53.

Gooding, R. M.
1984. Trapping surveys for the deep-water caridean shrimps *Heterocarpus laevigatus* and *H. ensifer* in the western Hawaiian Islands. Mar. Fish. Rev. 46(2):18–26.

Greenacre, M. J.
1984. Theory and applications of correspondence analysis. Academic Press, London, 364 p.

Houston, K. A., and R. L. Haedrich.
1984. Abundance and biomass of macrobenthos in the vicinity of Carson Submarine Canyon, northwest Atlantic Ocean. Mar. Biol. 82:301-305.

Hopkins, T. S.
1984. Physics of the sea. *In* R. Margalef (ed.), Western Mediterranean. Pergamon Press, Oxford, 363 p.

Jones, R.
1984. Assessing the effects of changes in exploitation using length composition data (with notes on VPA and cohort analysis). FAO Fish. Tech. Pap. 256:0–118.

Jones, S.
1969. The prawns fishery resources of India. FAO Fish. Rep. 57(3):725–748.

King, M. G.
1981. Increasing interest in the tropical Pacific's deep-water shrimps. Aust. Fish. 40(6):33–41.

King, M. G., and A. J. Butler.
1985. Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). Mar. Biol. 86:129–138.

Koslow, J. A., and A. Ota.
1981. The ecology of vertical migrations in the three common zooplankters in the La Jolla Bight, April–August 1967. Biol. Oceaonogr. 1:107–134.

Pérès, J. M.
1985. History of the Mediterranean biota and the colonization of the depths. *In* R. Margalef (ed.), Western Mediterranean. Pergamon Press, New York, p. 198–232.

Relini Orsi, L., and J. Relini.
1979. Pesca e riproduzione del gambero rosso *Aristeus antennatus* (Decapoda, Penaeoidae) nel Mar Ligure. Quad. Civica Staz. Idrobiol. Milano 7:1–39.

Relini, G., and L. Orsi Relini.
1987. The decline of red shrimp stocks in the Gulf of Genoa. Inv. Pesq. 51 (supl. 1): 245–260.

Reyss, D.
1971. Les canyons sous-marins de la mer Catalane: le rech du Cap et le rech Lacaze-Duthiers. III: Les peuplements de macrofaune benthique. Vie et Milieu 22:529–613.
1973. Les canyons sous-marins de la mer Catalane: le rech du Cap et le rech Lacaze-Duthiers. IV: Etude synécologyque des peuplements de macrofaune benthique. Vie et Milieu 23:101–142.

Risso, A.
1816. Historie naturelle des Crustacés des environs de Nice, 175 p.

Rowe, G. T.
1971. Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon. Deep-Sea Res. 18:569–581.

Sardà, F.
1993. Bio-ecological aspects of the fisheries of Crustacea Decapoda in the western Mediterranean. Aquat. Living Resour. 6:299–305.

Sardà, F., and J. E. Cartes.
1993a. Distribution, abundance and selected biological aspects of *Aristeus antennatus* in deep-water habitats in NW Mediterranean. B.I.O.S. (Thessaloniky, Greece) 1(1):59–73.
1993b. Relationship between size and depth in decapod populations on the slope between 900 and 2,200 m in the western Mediterranean. Deep-Sea Res. 4(11–12)2389–2400.

Sardà, F., and M. Demestre.
1987. Estudio biológico de la gamba *Aristeus antennatus* (Risso, 1816) en el Mar Catalán (NE de España). Inv. Pesq. 51 (1):213–232.
1989. Shortening of the rostrum and rostral variability in *Aristeus antennatus* (Risso, 1816) (Decapoda: Aristeidae). J. Crust. Biol. 9 (4):570–577.

Sardà, F., and P. Martin.
1986. Les pesqueries a Catalunya: evolució en els últims decennis. *In* J. Lleonart (ed.), L'Oceanografía, recursos pesquers de la mar Catalana. d'Ecol. Aplicada. Diputació de Barcelona 91–112.

Sardà, F., G. Y. Conan, and X. Fuste.
1993. Selectivity of Norway lobster (*Nephrops norvegicus*) in western Mediterranean. Sci. Mar. 57(2–3):167–174.

Sardà, F., C. Bas, and J. Lleonart.
In press. A functional morphometry of rose shrimp *Aristeus antennatus* (Risso, 1816) in western Mediterranean. Crustaceana.

Sousa, M. I.
1988. Sources of bias in growth and mortality estimation of migratory pelagic fish stocks, with emphasis on *Decapterus russelli* (Carangidae) in Mozambique. FAO Fish. Rep. 389:288–307.

Sparre, P., E. Ursin, and S. C. Venema.
1989. Introduction to tropical fish stock assessment. FAO Fish. Tech. Paper 306/1, 337 p.

Tobar, R., and F. Sardà.
1987. Análisis de la evolución de las capturas de gamba rosada, *Aristeus antennatus* (Risso, 1916), en los últimos decenios en Cataluña. Inf. Tec. del Inst. Ciencias del Mar de Barcelona (CSIC) 142:1–20.
1992. Annual and diel light cycle as a predictive factor in deep-water fisheries for the prawn *Aristeus antennatus* (Risso, 1816). Fish. Res. 15:169–179.

Tyler P. A.
1988. Seasonality in the deep sea. Oceanogr. Mar. Biol. Ann. Rev. 26:227–258.

Zar, J. H.
1984. Biostatistical Analysis. Prentice-Hall Inter., 718 p.

Predator-prey relationships of winter flounder, *Pleuronectes americanus*, in the New York Bight apex

Frank W. Steimle
Dorothy Jeffress
Stephen A. Fromm
Robert N. Reid
Joseph J. Vitaliano
Ann Frame

Sandy Hook Laboratory, Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA
Highlands, New Jersey 07732

Abstract.— A 39-month study of the effects of cessation of sewage sludge disposal in the New York Bight apex on the diets of certain fishes and on the benthic macrofaunal community provided an opportunity to examine predator-prey relationships of winter flounder, *Pleuronectes americanus*, one of the common predators in the area. Benthic macrofauna and winter flounder were collected monthly and bimonthly, respectively, from July 1986 through September 1989 at three sites in the Bight apex that are variably influenced by sewage sludge. There were limited changes in winter flounder diets and abundance of dominant benthic macrofaunal species following cessation of sewage sludge disposal. The comparison of volumetric contribution of common prey in flounder stomachs to potential-prey abundance in benthic samples suggested several relationships. These included evidence of preferential predation on the polychaete *Pherusa affinis*; this selective preference may be associated with its high caloric content as well as with its average high biomass density. Other common prey, primarily polychaetes but including an anthozoan, were also preyed upon in proportions greater than their abundance in the environment. Some moderately abundant potential prey, such as the small near-surface-dwelling mollusc *Nucula proxima* and the ribbon worm *Cerebratulus lacteus* were not commonly preyed upon suggesting they were unavailable as prey or were avoided by winter flounder. Corresponding fluctuations in abundances and predation of the pollution-tolerant polychaete *Capitella* sp. and the pollution-sensitive amphipod *Unciola irrorata* suggested a proportional consumption relationship in association with sludge disposal and its cessation.

Manuscript accepted 30 December 1993.
Fishery Bulletin 92:608–619 (1994).

Predator diets provide information on sources of prey, predominant prey types, levels of particular prey use and availability, and prey preference or avoidance, when compared with the availability of potential prey in the environment (Levings, 1974; Diehl, 1992). For predatory fish such as winter flounder, *Pleuronectes americanus*, this information increases our understanding of prey selection, based on evidence of prey preference or avoidance, and how selective predation can affect or be affected by prey population dynamics.

In studies of aquatic environmental health, benthic macrofaunal diversity and certain indicator species are often used as response variables. Monitoring predator diets during such studies can aid in determining how predation can function as a confounding factor in interpreting macrofaunal change as solely the product of altered abiotic factors. Monitoring diets can also indicate how benthic species abundance and the overall community structure can be affected by predation. Predation studies can also aid in estimating the effect of benthic macrofaunal changes (natural or anthropogenic) on predator-prey relationships (i.e. loss of a seasonally or energetically important prey) or be used to define potential contaminant uptake pathways (Clements and Livingston, 1982; Gendron, 1987; Schindler, 1987).

Studies of the linkage between prey abundance and predation by marine fish are scarce, especially studies based on samples taken over an extended period of time or during an environmental change. An opportunity to examine predator-prey relationships was provided by the availability of the results of a comprehensive 39-month study of the effects of sewage sludge disposal abatement in the New York Bight apex (the coastal area at the mouth of New York Harbor). This study included monitoring the diets of several common fishes and large decapod crustaceans, the abundance of benthic macrofauna, as well as other biological and environmental variables (Environmental Processes Div., 1988).

The winter flounder, *Pleuronectes americanus* Walbaum (Robins et al., 1991) is an abundant demersal fish in the New York Bight apex. It was the third most important contributor (10%) to the total fish biomass collected during the study (Wilk et

al., 1992). Winter flounder also rely almost entirely on small benthic macrofauna for food; thus, variability in predation and macrofaunal community structure can have important consequences for both the predator and its benthic prey (Kurtz, 1975; Clements and Livingston, 1982; Pihl et al., 1992).

This paper compares the diets of winter flounder with the abundance of benthic macrofauna at three stations in the New York Bight apex variably affected by sewage sludge, for evidence of 1) selective predation (preference or avoidance), 2) variation in the proportional consumption of benthic prey over time, and 3) the manner in which predator-prey relationships influenced the macrofauna with the cessation of sewage sludge disposal.

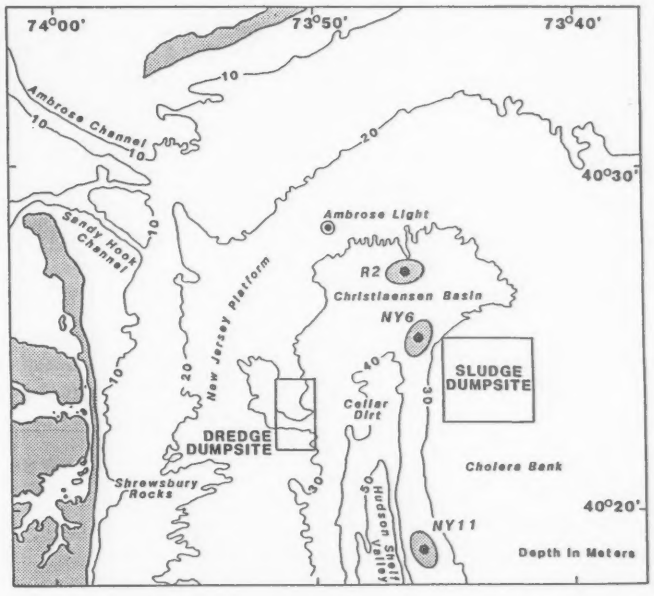


Figure 1

Location of stations and waste disposal sites in the New York Bight apex where winter flounder, *Pleuronectes americanus,* and benthic macrofauna were collected.

Materials and methods

Winter flounder and benthic macrofauna collection methods, sample processing, and primary data analyses for this study have been described in detail elsewhere (Reid et al. in press; Steimle, in press). In brief, three stations, R2, NY6, and NY11 (Fig. 1), were sampled systematically from July 1986 to September 1989 (Environmental Processes Div. 1988). These stations represent a gradient of conditions related to sewage sludge disposal, e.g. variable levels of total organic carbon (TOC) and chemical sediment contamination, such as chromium (Cr), that changed to some degree after cessation of disposal in December 1987 (Table 1). Station NY6 was the most sludge-affected area, with a markedly altered benthic community characterized by a relatively low species richness, low biomass, and high levels of TOC sediment contaminant such as Cr (Table 1). Station R2 was moderately affected by sludge and was biologically enhanced; it showed relatively high species richness and macrofaunal biomass and moderate levels of sediment contamination compared with NY6 (Table 1). Station NY11 was the least affected by sludge disposal, having relatively high species richness but low macrofaunal biomass and low levels of sediment contamination (Table 1). All stations were about 30 m in depth and had similar sediment types (silty-fine sands) and hydrographic characteristics (Table 1).

Triplicate benthic macrofaunal samples were collected monthly with a 0.1-m^2 Smith-McIntyre grab sampler and sieved through a 0.5-mm mesh screen. Materials retained were preserved in buffered formalin and later transferred to 70% ethanol. The samples were sorted and organisms were identified to the lowest possible taxon (usually species), counted, and moist-weighed (Reid et al., in press). Data from a total of 350 benthic macrofaunal samples were available for analysis.

Adult winter flounder were collected bimonthly (additional collections were made in August) with a small otter trawl at the same stations and during the same week as the benthic grab sampling. Each periodic trawl collection consisted of six daytime tows of 0.5 km, deployed in an array across the center of the station. Generally, at least 30 fish were collected from each station per collection period. Stomach contents were analyzed in the field or laboratory by using semi-quantitative, visual estimates of stomach volume from comparison of stomach boluses with variable-diameter, volume-calibrated cylinders. All identifiable items in the stomachs were identified to the lowest possible taxon and separated to visually estimate their individual percent contribution to total stomach volume (Langton et al., 1980; Steimle, in press). This method provides reasonable results compared with more labor intensive methods (Hyslop, 1980).

Table 1

Habitat characteristics (means) of three sampling sites in the New York Bight apex for the 18 months before (A) and 21 months after (B) sewage sludge disposal cessation; benthic biomass (wet wt) does not include the biomass of two large bivalves, *Pitar morrhuanus* and *Arctica islandica*.

	Stations					
	R2		NY6		NY11	
	A	B	A	B	A	B
Depth (m)	29		31		29	
Sediment						
grain size (phi)[1]	3.1	3.2	3.6	3.5	3.1	3.1
TOC (% dry wt)[1]	0.9	0.9	4.6	2.3	0.3	0.3
Cr (ppm dry wt)[2]	37.2	36.7	163.0	96.5	15.8	12.9
Bottom water[3]						
min. dissolved oxygen (mg/L)	4.2	5.7[4]	4.3	5.8[4]	5.3	5.5[4]
temp. range (°C)	~3–17 for all sites[5]					
Benthos						
biomass (g/m^2)	218.2	202.8	63.4	28.2	66.6	73.2
species (n)/grab	30	33	19	33	41	45

[1] Packer et al., in press.
[2] Zdanowicz et al., in press.
[3] Arlen, L., A. Draxler, and R. Bruno. Hydrographic observations in the bottom water of the New York Bight at the "12 mile" dumpsite: 1983–1990. Unpubl. manuscr.
[4] Dissolved oxygen content of <3 mg/L was recorded in September, 1989.
[5] Summer levels in 1988 were 2–3°C lower than the long-term mean.

The mean proportional volume (percent of the total volume) of a given prey item in the stomach was compared with the mean proportional biomass of that prey in the benthic macrofauna, and the relationship between these proportions was used to determine whether selective predation was evident. Although this approach to examining predator-prey associations differs from the traditional use of prey numerical abundance in stomachs and the environment, it is nonetheless realistic and useful because 1) prey volume can be a more precise dietary variable compared with uncertain enumeration of prey that are easily fragmented and for which only parts are present and 2) volume and biomass are approximately equivalent for most common prey taxa (see below). However, amphipods were also considered numerically because they are usually eaten whole and their exoskeletons are resistant to digestion and thus allow a reasonably accurate assessment of the number of individuals eaten.

The stomachs of 3,556 adult winter flounder, 18–30 cm total length, examined from the three study sites had identifiable food in them. To examine overall predator-prey relationships, stomach content and benthic data from the entire study period were pooled for each station because there were only minor changes in dominant prey and benthic species associated with sludge disposal cessation (Reid et al., in press; Steimle, in press). The use of pooled stomach content data to estimate prey preference by a predator population is recommended by some authors, e.g. Rachlin et al. (1987). Changes in predator-prey relationships related to cessation of sludge disposal are considered separately. Any seasonal or annual variability was assumed to be distributed equally within the pooled data as there were no gaps in collections. Log transformation of Shorigin's forage ratio index ($K=rt/pt$), adapted from a numerical approach for prey volume and biomass, was used to estimate prey selectivity (Berg, 1979): $K' = \mathrm{Log}_{10}(rt/pt)$, where rt = proportion of prey in the diet estimated by contribution to stomach volume and pt = proportion of prey in the benthic biomass. Positive K' values suggest a degree of selective predation. Near-zero K' values suggested that predation is directly proportional to abundance. Negative K' values suggest underutilization or avoidance of a potential prey relative to its availability.

The use of volume and biomass to calculate K' is reasonable because 1 mL or cm^3 of prey volume is considered approximately equivalent to 1 g of macrofauna wet weight (Bowman, 1986). We partially verified this assumption by determining the mean volume to wet weight ratios for a number of individuals for a range of common prey taxa. The ratios for an

anthozoan, *Ceriantheopsis americanus*, a polychaete, *Pherusa affinis*, and the sand shrimp *Crangon septemspinosa* varied between 0.96 and 1.00 (n=≥26). However, the ratios for calcareous-shelled prey were lower, 0.70 for the bivalve mollusc *Nucula proxima* (n=50), and 0.77 for the sand dollar *Echinarachnius parma* (n=30).

All fish were collected near mid-day; therefore, the effects of digestion on stomach volume estimates were not considered a major factor. Winter flounder are primarily daytime feeders and all but the most soft-bodied prey should remain identifiable in their stomachs for several hours (MacDonald et al., 1982).

Results

Diet spectrum and dominance

Forty-nine prey taxa were identified in winter flounder stomachs, although only about 30 taxa were identified in the stomach contents at any individual station (Table 2). These are conservative estimates because of some uncertainties in identification caused by digestion. This prey spectrum represents about a quarter of the total available benthic macrofaunal taxa identified at station NY6 (119 species) and R2 (133 species), and about a fifth of the 154 species identified at station NY11.

Dominant prey, defined as species that composed at least 2% of the total stomach volume of fish from any station, were the polychaetes *Pherusa affinis*, *Asabellides oculata*, and *Nephtys incisa* and the tube-dwelling anthozoan *Ceriantheopsis americanus*. The rhynchocoel *Cerebratulus lacteus*, juvenile rock crabs *Cancer irroratus*, and other polychaetes, including *Capitella* sp. and *Scoletoma (Lumbrineris)* spp., were dominant in the diet at one or two stations (Table 3). Collectively these eight taxa constituted between 76% and 96% of the winter flounder diet by volume at the three stations (Table 3).

Predation patterns

The log forage ratio (K') indices were positive for several dominant species. The K' index was consistently high (≥+0.25) for the polychaetes, *P. affinis* and *A. oculata*. High positive K' values were also calculated for other prey, but at only one or two stations (Table 3). The K' indices were near zero (±0.20) for some dominant species at some stations, such as *C. americanus*. For other prey or at other stations the K' indices were low (<–0.25). This was especially evident for *C. americanus, Spio setosa, Glycera* sp., and the molluscs (Table 3).

Comparison of the contributions of these dominant prey species to flounder diets and to macrofaunal

Table 2

List of winter flounder, *Pleuronectes americanus*, prey identified in stomachs collected from three stations in the New York Bight apex.

	Station		
Prey	R2	NY6	NY11
Algae	X	X	
Coelenterates			
Ceriantheopsis americanus	X	X	X
Hydrozoans	X		X
Rhynchocoels	X	X	X
Nematodes		X	
Chaetognaths			X
Bryozoans		X	
Molluscs			
Nucula proxima	X	X	X
Yoldia sp.			X
Nudibranchia			X
Ilyanassa trivittata		X	
Polychaetes			
Nephtys sp.	X	X	X
Nephtys incisa	X	X	X
Ninoe nigripes	X		
Scoletoma (Lumbrineris) sp.	X	X	X
Scoletoma acicularum			X
Pherusa affinis	X	X	X
Asabellides oculata	X	X	X
Ampharete acutifrons		X	
Spionidae		X	X
Spio setosa	X		X
Spiophanes bombyx	X	X	X
Cirratulus cirratus		X	
Tharyx sp.	X		
Tharyx acutus	X	X	X
Capitella sp.	X	X	X
Mediomastus ambiseta	X		
Phyllodoce arenae	X		X
Drilonereis sp.	X	X	X
Glycera sp.	X	X	X
Ophioglycera gigantea	X		
Chone infundibuliformis			X
Aglaophamus circinata	X		
Nereis succinea		X	
Isopods			
Edotea triloba	X	X	X
Cirolana sp.		X	
Cumaceans			
Diastylis sp.	X	X	X
Amphipods			
Leptocheirus pinguis	X	X	X
Unciola irrorata	X	X	X
Monoculodes edwardsi		X	X
Photis pollex			X
Dyopedos sp.		X	
Mysids	X		
Decapods			
Cancer sp.	X	X	X
Cancer irroratus	X	X	X
Crangon septemspinosus	X	X	X
Echinoderms			
Echinarachnius parma			X
Tunicates			
Molgula sp.	X		
Salpidae		X	X

Table 3

Comparison of the average contribution of dominant prey in the diet of winter flounder, *Pleuronectes americanus* (mean % total stomach volume), to that of prey and dominant benthic infauna (infn) species (mean % total wet weight biomass) at stations in the New York Bight apex, 1986–1989. Seventy two benthic grab samples (triplicate samples at 24 collection periods) are included. K' is the log forage ratio.

	Stations								
	NY6			R2			NY11		
Species	prey	infn	(*K'*)	prey	infn	(*K'*)	prey	infn	(*K'*)
Ceriantheopsis americanus	28.0	18.5	0.18	7.0	6.6	0.03	27.3	6.4	0.63
Pherusa affinis	25.1	2.7	0.97	76.3	42.8	0.25	48.3	9.7	0.70
Asabellides oculata	9.2	3.8	0.38	3.4	<0.1	>1.83	2.0	<0.1	>1.60
Nephtys incisa	3.5	3.5	0	4.9	4.9	0	2.0	0.7	0.46
Capitella sp.	6.0	11.7	–0.29	0.3	<0.1	>0.78	<0.1	<0.1	0
Cerebratulus acteus	3.0	45.3	–1.15	2.4	2.0	0.08	0.8	2.0	–0.40
Scoletoma sp.	1.5	<0.1	>1.48	2.1	<0.1	>1.62	4.1	3.3	0.09
Cancer irroratus	11.3	2.4	0.67	1.5	4.4	–0.47	1.2	0.3	0.60
Spio setosa	<0.1	0.6	<–1.10	<0.1	0.1	<–0.30	0.8	7.5	–0.96
Nucula proxima	0.1	1.9	–1.30	<0.1	0.5	<–1.00	0.1	6.6	–1.70
Glycera sp.	0.6	0.8	–0.12	<0.1	0.2	<–0.60	0.1	6.5	–1.70
Pitar morrhuanus	0.0	0.1	–∞	0.0	30.7	–∞	0.0	14.7	–∞
Arctica islandica	0.0	0.1	–∞	0.0	<0.1	–∞	0.0	28.1	–∞
Ensis directus	0.0	<0.1	–∞	0.0	3.1	–∞	0.0	<0.1	–∞
Totals	78.2[1]	91.8		97.9	95.3		86.6	85.8	
Nonempty stomachs (*n*)		1405			1628			523	

[1] Diet residuals at this station were primarily (~11%) unidentifiable organic and inorganic material.

biomass over time illustrates trends in the predator-prey association not evident in the pooled data (Table 3). For example, there was an apparent proportional consumption association (level of prey consumption was closely associated with level of abundance) for the anemone *C. americanus* at all stations, although the strength of the association varied at times (Fig. 2).

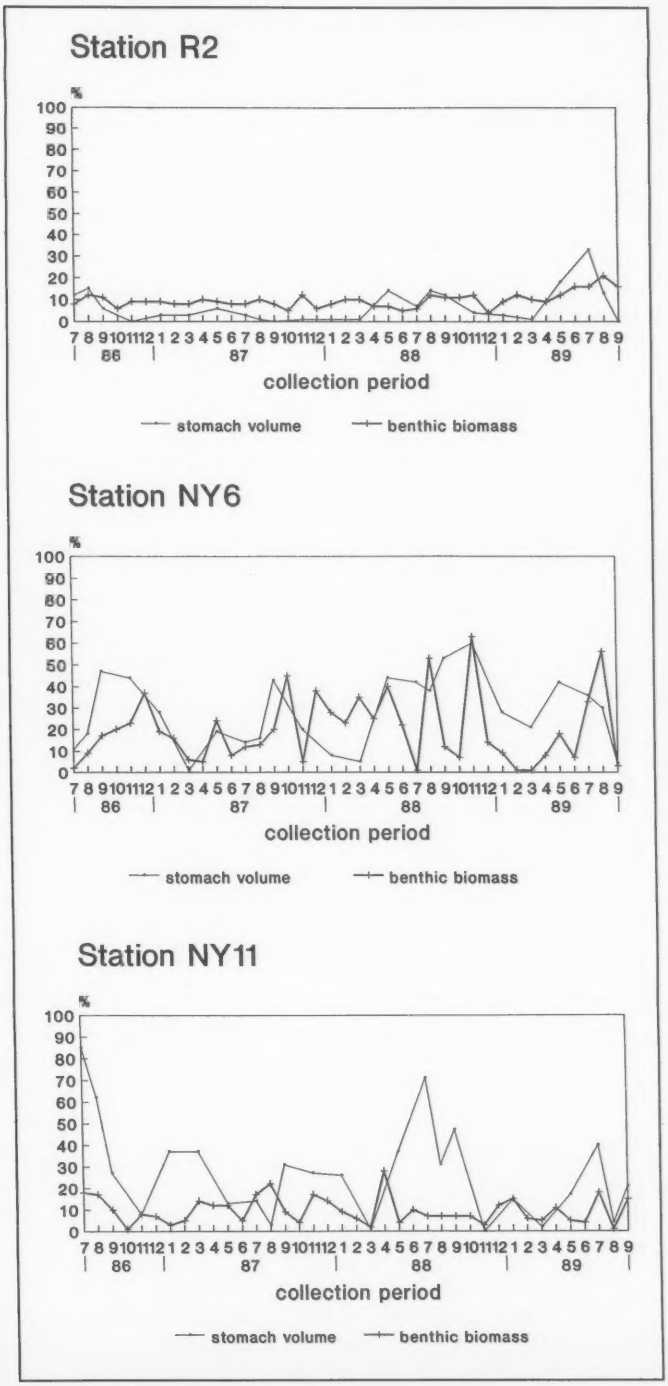
However, the proportional contribution of the polychaete *P. affinis* to winter flounder diets was greater than the prey's proportional contribution to total benthic macrofaunal biomass (Table 3, Fig. 3). The contribution of this prey to the winter flounder diet generally paralleled its contribution to macrofaunal biomass at all stations during the study period. Peaks in consumption are often consistent with peaks in proportional contribution to total community biomass, especially at stations NY6 and NY11 (Fig. 3). For the entire study period, the difference in proportional consumption and biomass for *P. affinis* ranged from 9.3 fold at station NY6 (25.1% stomach volume vs. 2.7% benthic biomass; K'=0.97) to 1.8 fold at station R2 (76.3% volume vs. 42.8% biomass; K'=0.25); station NY11 had an intermediate difference of 3.7 fold and K'=0.70 (Table 3).

Some benthic species that were dominant in the overall benthic biomass were seldom identified in the flounder stomachs. For example, the rhynchocoel *C. lacteus,* which was particularly abundant at station NY6, was not often found in flounder stomachs, despite its relative importance in the benthic biomass (Table 3). This underutilization of potential prey was also evident at station NY11, where the polychaetes, *Glycera* spp. (mostly *G. dibranchiata*) and *Spio setosa*, as well as several mollusc species, composed >5% of the mean macrofauna biomass but were never important items in the flounder diet (Table 3). However, a substantial portion of the small, unidentified polychaete fragments found in some winter flounder stomachs may have been *S. setosa*. The predation-abundance trends over the study period for these and other less common prey are not presented but were similar to the trends presented for *C. americanus* (Fig 2).

In general, there was little evidence of predation on molluscs by winter flounder, despite their sometimes high contribution to overall macrofaunal biomass. For example, the minute (<5 mm shell width) Atlantic nut clam, *Nucula proxima*, a consistent, although only moderate component of the infaunal biomass, was not commonly found in winter flounder stomachs (Table 3).

Cessation of sewage sludge disposal

The change in abundance of two benthic species, the polychaete *Capitella* sp. and the amphipod *U. irrorata*, was associated with the cessation of sludge disposal (Reid et al., in press). These changes were also reflected in the occurrence of these two prey in winter flounder stomachs. When sludge disposal ended in 1987, the abundance of the stress-tolerant *Capitella* sp. declined and so did its occurrence in stomachs at station NY6 (Fig 4). For the more stress-sensitive *U. irrorata*, predation was also generally associated with abundance at two stations (Fig. 5). At station NY6, where the effect of sludge disposal was greatest, the abatement of sludge disposal was accompanied by a seasonally varying increase in the abundance of this amphipod and a corresponding increase in the frequency of occurrence in winter flounder stomachs (Fig. 5).



Discussion

Diet spectrum and dominance

The spectrum of prey and dominant prey taxa consumed by winter flounder in the New York Bight apex (Table 2) is similar to that reported in other winter flounder diet studies (Wells et al., 1973; Hacunda, 1981; Langton and Bowman, 1981; Bharadwaj, 1988; Steimle and Terranova, 1991). Winter flounder diet studies in estuaries and to the north also report the dominance of similar prey taxa (Tyler, 1972; Wells et al., 1973; Worobec, 1982). With the possible exception of *Capitella* sp., dominant prey are usually macroscopic, supporting Keats' (1990) hypothesis that winter flounder show a preference for the largest available prey that can be consumed.

Predation patterns

The results of this study provide evidence that some prey species are consumed preferentially, but this was not temporally or spa-

Figure 2

Trends in the percent contribution of the burrowing anemone *Ceriantheopsis americanus* to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the anemone's percentage of the total benthic macrofaunal biomass at three sites in the New York Bight apex variably affected by sewage sludge disposal. Disposal gradually abated during 1987 and ceased by December 1987.

tially consistent. The parallel temporal relationship of the contribution of the anemone *C. americanus* to overall benthic biomass and to winter flounder diets at stations R2 and NY6 (Fig. 2) suggests a proportional consumption association. The forage ratio indices (K') for this prey are near zero (0.03 to 0.18, Table 3); these suggest that winter flounder neither preferred nor avoided this prey, consuming it at a level closely related to its availability at these two stations. Although, this relation was more variable at station NY11 (Fig. 2), a moderately high, positive K' value (0.63) suggests some preference for this prey (Table 3).

The proportional consumption differences (Fig. 3) and strong positive K' values at each station for *P. affinis* (Table 3) strongly suggest that winter flounder have a preference for this prey. Heavy predation on *P. affinis* may be energetically advantageous to winter flounder because this species has a high caloric equivalence ($\bar{x}$=1.9 Kcal/g wet weight; Steimle and Terranova, 1985). This is about double that of other major prey, which range from 0.9 to 1.1 Kcal/g wet weight, although some amphipod species, such as *U. irrorata* (consumed to a minor extent), are equally energy rich (Steimle and Terranova, 1985). The energy content of prey has been discussed as an important consideration in optimum foraging theories (Mangel and Clark, 1986) and the winter flounder preference for this high energy prey provides support for these theories. It is also possible that preference for this prey is related to the long-term dominance of *P. affinis* in the macrofauna of siltier areas of the New York Bight apex, as this relatively productive species has been common in the area and has been preyed upon since at least the mid-1960's (Steimle and Stone, 1973; Steimle, 1985, 1990; Steimle et al., 1990). This extended period of dominance may have contributed to winter flounder becoming experienced predators on this species (and other abundant prey species) and thus maintaining the preference (Gendron, 1987).

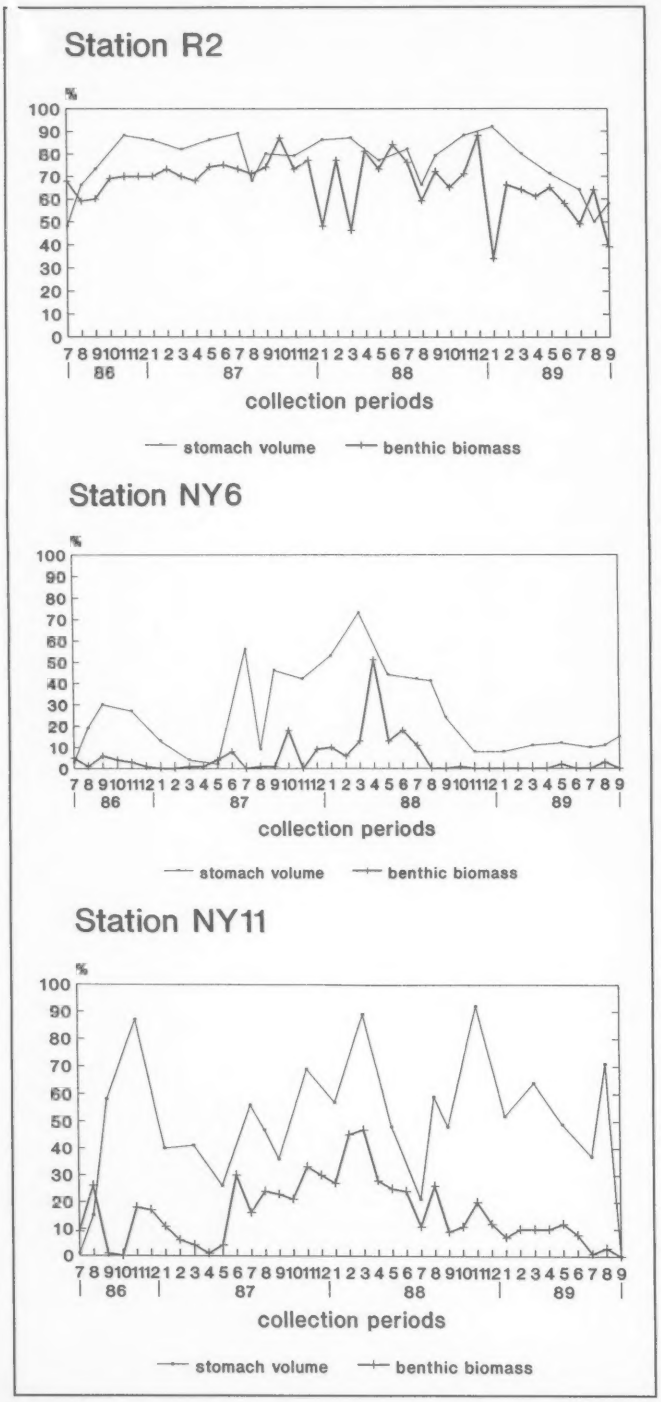


Figure 3

Trends in the percent contribution of the polychaete *Pherusa affinis* to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the polychaete's percentage contribution of the total benthic macrofaunal biomass at three sites in the New York Bight apex variably affected by sewage sludge disposal.

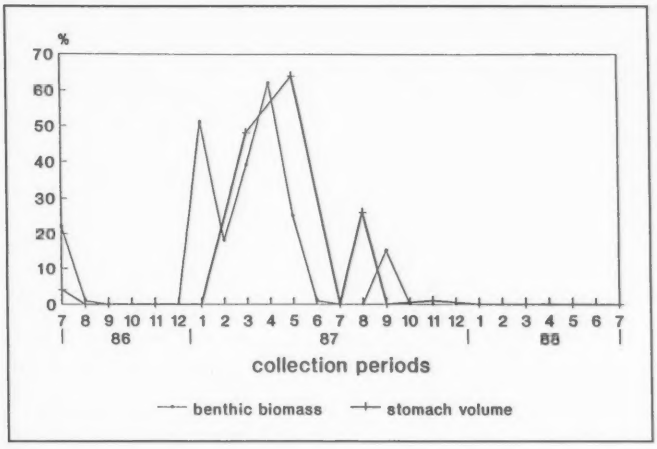
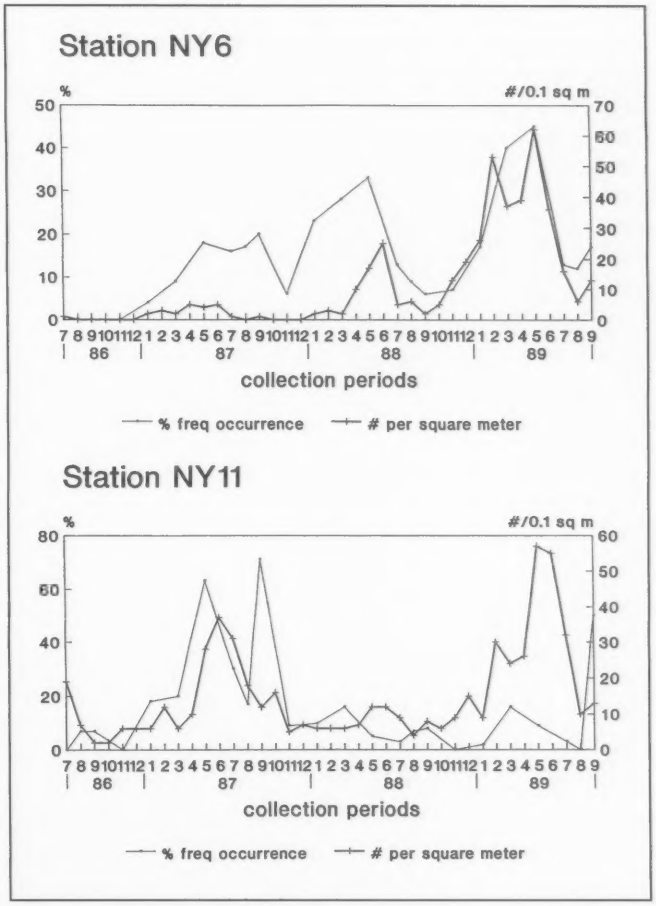


Figure 4

Trends in the percent contribution of the pollution-tolerant polychaete *Capitella* sp. to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the polychaete's percentage contribution to total benthic macrofaunal biomass at NY6, the station most affected by sewage sludge disposal and its cessation, in the New York Bight apex.

Figure 5

Trends in the frequency of occurrence of the amphipod *Unciola irrorata* in the diet of winter flounder, *Pleuronectes americanus*, compared to its numerical abundance in the benthic macrofaunal community at two stations in the New York Bight apex variably affected by sewage sludge disposal and its cessation in December 1987.



With the exception of *P. affinis* and perhaps *C. irroratus*, there is limited evidence of prey preference by winter flounder. This is consistent with the results of many qualitative winter flounder feeding studies that report a diverse diet, but also with limited evidence of a prey species' preferences (Tyler, 1972; Klein-MacPhee, 1978; Keats, 1990).

However, several dominant members of the benthic macrofaunal community at the three study stations were not commonly consumed by winter flounder. This underutilization may be related to prey size, burrowing depth, defense or escape mechanisms, or a variety of other factors (Main, 1985). For example, there was limited predation on *C. lacteus*, a major contributor to benthic biomass at station NY6. This nonproportional consumption or possible "avoidance" of this species is evident in the difference between the proportional consumption and abundance levels at this station (3.0% stomach volume vs. 45.3% benthic biomass) and the strong negative K' (–1.15; Table 3); this difference at NY6 was fairly consistent over the study period (Fig. 6). Proportional predation or slight underutilization of this prey was evident at the other stations where it was less abundant and K' ranged from +0.08 to –0.40 (Table 3).

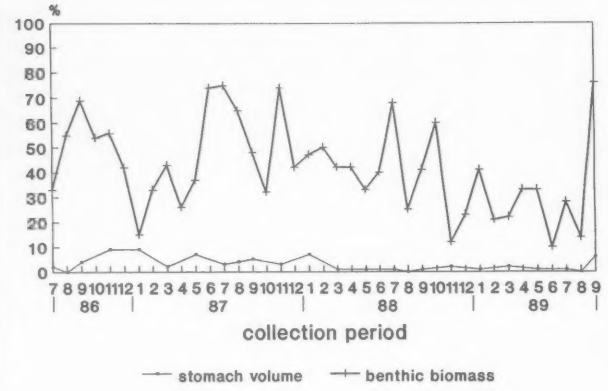


Figure 6

Trends in the percent contribution of the rhynchocoel *Cerebratulus lacteus* to the total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the rhynchocoel's percentage contribution to total benthic macrofaunal biomass at NY6, the station most affected by sewage sludge disposal and its cessation, in the New York Bight apex.

The limited predation on *C. lacteus* could be related to its possession of defensive toxins in its tissues or to secretion of mucus that is strongly acidic, both of which can be offensive to potential predators (Kem, 1985; McDermott and Roe, 1985). Paradoxically, rhynchocoels are collected for fish bait in some areas and eaten by other fishes. It is possible, however, that this rhynchocoel's large size (>100 cm in length and >2 cm in width; Gosner, 1971), not its reported toxicity, is responsible for its limited use as prey for the small-mouthed winter flounder.

The underutilization of the small bivalve mollusc *N. proxima* (Table 3) is probably the result of its lack of availability as this species burrows into the sediment. The other molluscs common in the area, such as *P. morrhuanus*, *A. islandica*, *Ilyanassa trivittata*, and *Ensis directus*, are probably either too large or deeply buried to be suitable prey for winter flounder. However, *N. proxima*, as well as these other molluscs, except *P. morrhuanus*, were noted as prey in the diets of winter flounder elsewhere (Kurtz, 1975; Gilbert and Suchow, 1977; Klein-MacPhee, 1978; MacDonald et al., 1982; Worobec, 1982). The molluscan contribution to winter flounder diets in Narragansett Bay, Rhode Island, was also considered negligible (Bharadwaj, 1988).

Cessation of sewage sludge disposal

The cessation of sewage sludge disposal was expected to result in a substantial change in abundance of disposal-sensitive species in the benthic macrofaunal community. Any macrofaunal changes because of cessation were expected to be reflected in some predation variables (Spies, 1984; Cross et al., 1985; Environmental Processes Division, 1988). However, the only significant changes in the benthic community detected after cessation from 1987 to 1990 were in the overall abundance of a few pollution-tolerant or pollution-sensitive taxa, such as the polychaete *Capitella* sp. or amphipods at station NY6, nearest to the former disposal area. The abundance of other dominant benthic species at NY6, such as *P. affinis*, *N. incisa*, and *C. americanus*, did not change to any significant degree (Reid et al., in press).

The pollution-tolerant *Capitella* sp. has been a consistent, but variably abundant (hundreds to tens of thousands of individuals/m^2), member of the degraded benthic community at station NY6 since at least the early 1970's (Caracciola and Steimle, 1983). Its density in the macrofauna declined drastically (<100 individuals/m^2) after the cessation of sewage sludge disposal (Reid et al., 1991). Predation by winter flounder on this prey is probably related to the response of *Capitella* sp. to cessation of disposal.

There were increases in abundance of contaminant-sensitive amphipods, especially *Photis pollex* and *U. irrorata*, at station NY6 after disposal abatement began in 1987. Although contributions of amphipods to winter flounder diets were generally less than 1% of total stomach volumes (and thus not included in Table 3), numerical increases in amphipod abundance in the macrofaunal community coincided with increases in their frequency of occurrence in winter flounder stomachs. The general increase in the numerical abundance of one amphipod, *U. irrorata*, in benthic samples at NY6, especially after cessation, was accompanied by a corresponding increase in their occurrence in winter flounder stomachs (Fig. 5). However, a similar predation relationship for this prey was somewhat evident at station NY11, which was minimally affected by sludge disposal and cessation (Fig. 5). At both stations, the frequency of occurrence of *U. irrorata* in the diets closely paralleled seasonal (winter-spring) peaks in abundance, including reduced predation during an apparently poor recruitment year at NY11 in 1988 (Fig. 5). If the effects of the sludge were more general and included some effect at NY11, the pattern of predation on this species, which increased in abundance after cessation, could be associated with this cessation.

Predation influence on benthic populations and energetics

Strong selective predation by winter flounder on certain benthic macrofaunal taxa can influence the population dynamics of these prey and be a factor in interpreting benthic community change relative to disposal abatement. This affect may be evident in the predation-abundance patterns for *Capitella* sp., although the decline in the abundance of this species could be a result of its short life span as well as predation.

A short life span is not a factor for *P. affinis* as it lives for up to two years (Steimle et al. 1990). However, since winter flounder are visual predators (Klein-MacPhee, 1978; Bharadwaj, 1988), *P. affinis* may be at greater risk to predation because it is relatively large (up to 7.5 cm in length and 0.5 cm in width) and lives in vertical burrows with its fanned, setaceous cephalic cage (head and bristles) usually exposed. It also actively probes the sediment surface with feeding palps that may attract predator attention (J. Vitaliano, personal observ.; P. Ferri[1]). The persistent abundance and strong predation on *P. affinis* by winter flounder (Fig. 3) and other predators at station R2 (Steimle and Terranova, 1991; Steimle, in press) is interesting in that it suggests that this prey must be very productive in this area to sustain heavy predation pressure. This suggestion is supported by results of a previous study of the secondary production of this species that found it to be almost twice as productive near R2 as at NY6 and NY11 (Steimle et al., 1990).

The results of this study are subject to potential biases inherent in most stomach content analyses, such as differential digestion of different prey types (MacDonald et al., 1982). Partial digestion of prey can underestimate a prey's contribution to diets based on stomach volume. Thus, the estimated proportional contribution to diets of some soft-bodied prey will be conservative. This study also assumes that the stomach contents of fish represented feeding at or very near where the benthic infauna samples were collected (Steimle, in press) and that if a large proportion of the prey was consumed in nearby areas, the benthic community structure did not differ substantially from that at the actual benthic collection site. Some preliminary data from peripheral benthic stations sampled during the study suggest that this assumption was valid, although there were substantial changes in community structure in some parts of the trawling zones (Fromm, personal observ.).

[1] Ferri, P., U.S. Environmental Protection Agency, Narragansett, RI 02882. Personal Commun., 1992.

In summary, diets of winter flounder in the New York Bight apex 1) were dominated by a few prey species, typically polychaetes, an anthozoan, and small crustaceans; 2) showed a preference for the energy-rich polychaete *Pherusa affinis*; 3) suggested there was underutilization or "avoidance" of molluscs and rhynchocoels; and 4) showed that apparent responses of some benthic macrofaunal species (*Capitella* sp. and *U. irrorata*) to cessation of sludge disposal and natural fluctuations in abundance were reflected in corresponding changes in their use as prey.

Acknowledgments

We thank S. Fromm, C. Zetlin, and R. Koch for their contribution to data processing and graphics, and D. Packer, S. Chang, D. Mountain, and others for helpful comments and suggestions.

Literature cited

Berg, J.
1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. 50:263–273.

Bharadwaj, A.
1988. The feeding ecology of the winter flounder, *Pseudopleuronectes americanus* (Walbaum), in Narragansett Bay, Rhode Island. M.S. thesis, Univ. Rhode Island, Kingston, RI, 129 p.

Bowman, R. E.
1986. Effects of regurgitation on stomach content data of marine fishes. Environ. Biol. Fish. 16:171–181.

Caracciola, J. V., and F. W. Steimle.
1983. An atlas of the distribution and abundance of dominant benthic invertebrates in the New York Bight apex with reviews of their life histories. NOAA Tech. Rep. NMFS SSRF-766, 58 p.

Clements, W. H., and R. J. Livingston.
1982. Overlap and pollution-induced variability in the feeding habits of filefish (Pisces: Monacanthidae) from Apalachee Bay, Florida. Copeia 2:331–338.

Cross, J. N., J. Roney, and G. S. Kleppel.
1985. Fish food habits along a pollution gradient. Calif. Fish Game 71:28–39.

Diehl, S.
1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646–1661.

Environmental Processes Division.
1988. Plan for study-response of habitat and biota of the inner New York Bight to abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/NEC-55, 34 p.

Gendron, R. P.
1987. Models and mechanisms of frequency-dependent predation. Am. Nat. 130:603–623.

Gilbert, W. H., and E. F. Suchow.
1977. Predation by winter flounder (*Pseudopleuronectes americanus*) on the siphons of the clam, *Tellina agilis*. Nautilus 91:16–17.

Gosner, K. L.
1971. Guide to identification of marine and estuarine invertebrates, Cape Hatteras to the Bay of Fundy. Wiley-Interscience, NY, 693 p.

Hacunda, J. S.
1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fish. Bull. 79:775–788.

Hyslop, E. J.
1980. Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17:411–423.

Keats, D. W.
1990. Food of winter flounder *Pseudopleuronectes americanus* in a sea urchin dominated community in eastern Newfoundland. Mar. Ecol. Prog. Ser. 60:13–22.

Kem, W. R.
1985. Structure and action of nemertean toxins. Am. Zool. 25:99–111.

Klein-MacPhee, G.
1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). NOAA Tech. Rep. NMFS Circ. 414, 43 p.

Kurtz, R. J.
1975. Stomach content analysis in relation to differences in growth rate of winter flounder (*Pseudopleuronectes americanus*) from two Long Island Bays. M.S. thesis, Long Island Univ., Greenvale, NY, 60 p.

Langton, R. W., and R. E. Bowman.
1981. Food of eight northwest Atlantic pleuronectiform fishes. NOAA Tech. Rep. SSRF-749, 16 p.

Langton, R. W., B. M. North, B. P. Hayden, and R. E. Bowman.
1980. Fish food habits studies—sampling procedures and data processing methods utilized by the Northeast Fisheries Center, Woods Hole Laboratory, USA. Int. Counc. Explor. Sea, C. M. 1980/L:61, 16 p.

Levings, C. D.
1974. Seasonal changes in feeding and particle selection by winter flounder (*Pseudopleuronectes americanus*). Trans. Am. Fish. Soc. 103:828–832.

MacDonald, J. S., K. G. Waiwood, and R. H. Green.
1982. Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*) and American plaice (*Hippoglossoides platessoides*). Can. J. Fish. Aquat. Sci. 39:651–659.

Main, K. L.
1985. The influence of prey identity and size on selection of prey by two marine fishes. J. Exp. Mar. Biol. Ecol. 88:145–152.

Mangel, M., and C. W. Clark.
1986. Towards a unified foraging theory. Ecology 67:1127–1138.

McDermott, J. J., and P. Roe.
1985. Food, feeding behavior and feeding ecology of nemerteans. Am. Zool. 25:113–125.

Packer, D., T. Finneran, L. Arlen, R. Koch, S. Fromm, J. Finn, S. A. Fromm, and A. Draxler.
In. Press. Fundamental and mass properties of surficial sediments in the inner New York Bight and responses to the abatement of sewage sludge dumping. *In* A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Pihl, L., S. P. Baden, R. J. Diaz, and L. C. Schaffner.
1992. Hypoxia-induced structural changes in the diets of bottom-feeding fish and Crustacea. Mar. Biol. 112:349–361.

Rachlin, J. W., A. Pappantoniou, and B. E. Warkentine.
1987. A bias estimator of the environmental resource base in diet preference studies with fish. J. Freshwater Ecol. 4:23–31.

Reid, R., D. Radosh, A. Frame, and S. Fromm.
1991. Benthic macrofauna of the New York Bight, 1979–89. NOAA Tech. Rep. NMFS 103, 50 p.

Reid, R., S. Fromm, A. Frame, D. Jeffress, J. Vitaliano, D. Radosh, and J. Finn.
In press. Limited responses of benthic macrofauna and selected sewage sludge components to phase-out of sludge dumping in the inner New York Bight. *In* A. Studholme, J.E. O'Reilly, and M.C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott.
1991. Common and scientific names of fishes from the United States and Canada (5th ed.). Am. Fish. Soc. Spec. Publ. 20.

Schindler, D. W.
1987. Detecting ecosystem responses to anthropogenic stress. Can. J. Fish. Aquat. Sci. 44 (Suppl.1): 6–25.

Spies, R.
1984. Benthic-pelagic coupling in sewage-affected marine ecosystems. Mar. Environ. Res. 13:195–230.

Steimle, F.
1985. Biomass and estimated productivity of the benthic macrofauna in the New York Bight: a stressed coastal area. Estuarine Coastal Shelf Sci. 21:539–554.
1990. Benthic macrofauna and habitat monitoring on the continental shelf of the northeastern United

States. I: Biomass. NOAA Tech. Rep. NMFS 86, 28 p.

Steimle, F. W.
In press. Effects of sewage sludge disposal abatement on winter flounder, red hake, and lobster feeding and diets in the New York Bight Apex. *In* A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Steimle, F. W., and R. B. Stone.
1973. Abundance and distribution of inshore benthic fauna off southwestern Long Island, N.Y. NOAA Tech. Rep. NMFS SSRF-673, 50 p.

Steimle, F. W., and R. Terranova.
1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. J. Northwest Atl. Fish. Sci. 6:117–124.
1991. Trophodynamics of select demersal fishes in the New York Bight. NOAA Tech. Memo. F/NEC-84, 11 p.

Steimle, F. W., P. Kinner, S. Howe, and W. Leathem.
1990. Polychaete population dynamics and production in the New York Bight associated with variable levels of sediment contamination. Ophelia 31:105–123.

Tyler, A. V.
1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Board Can. 29:997–1003.

Wells, B. D., D. H. Steele, and A. V. Tyler.
1973. Intertidal feeding of winter flounder (*Pseudopleuronectes americanus*) in the Bay of Fundy. J. Fish. Res. Board Can. 30:1374–1378.

Wilk, S., R. Pikanowski, A. Pacheco, D. MacMillan, and L. Stehlik.
1992. Response of fish and megainvertebrates of the New York Bight apex to the abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/NEC-90, 78 p.

Worobec, M. N.
1982. Field analysis of winter flounder *Pseudopleuronectes americanus* in a coastal pond: abundance, daily ration, and annual consumption. Ph.D. thesis, Univ. Rhode Island, Kingston, RI, 115 p.

Zdanowicz, V. S., S. L. Cunneff, and T. W. Finneran.
In press. Reductions in sediment metal contamination in the New York Bight apex with the cessation of sewage sludge dumping. *In* A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington

Kenneth L. Weinberg

Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way N.E., Seattle, WA 98115-0070

Abstract.—Numerical classification techniques, recurrent group analysis, and a clustering analysis that uses the Bray-Curtis resemblance measure were used to identify rockfish (family Scorpaenidae) assemblages in the offshore waters of Oregon and Washington. Catch data from six multispecies groundfish assessment surveys conducted at three-year intervals (1977–92) by the National Marine Fisheries Service's Alaska Fisheries Science Center revealed three assemblages. The first, a deep-water assemblage, consisted of shortspine thornyhead, *Sebastolobus alascanus*, Pacific ocean perch, *Sebastes alutus*, darkblotched rockfish, *S. crameri*, and splitnose rockfish, *S. diploproa*. Redbanded rockfish, *S. babcocki*, and rougheye rockfish, *S. aleutianus*, were closely associated with this group. The second assemblage consisted of canary rockfish, *S. pinniger*, yellowtail rockfish, *S. flavidus*, and greenstriped rockfish, *S. elongatus*. This group was most abundant in areas over the middle shelf. The third assemblage, closely associated with the second, consisted of sharpchin, *S. zacentrus*, rosethorn, *S. helvomaculatus*, and redstripe, *S. proriger*, rockfish. While the three assemblages may be of particular interest to ecologists, managers faced with the division of the *Sebastes* complex management unit into groups that better reflect rockfish cooccurrence may only be able to manage the latter two assemblages as one shelf-rockfish unit.

Manuscript accepted 4 January 1994.
Fishery Bulletin 92:620–632 (1994).

Over the last three decades, some stocks of the more than 30 species of rockfish (family Scorpaenidae) known to inhabit the offshore waters of Oregon and Washington (Eschmeyer and Herald, 1983) have been the target of intense foreign and domestic fishing pressure in a largely multispecies trawl fishery. In 1982 a groundfish fishery management plan was implemented by the Pacific Fisheries Management Council to address the reductions in groundfish populations, including serious declines of several rockfish species in some areas. This plan was based on an underlying single-species management philosophy.

In both the Columbia and the U.S. portion of the Vancouver (US-Vancouver) management areas instituted by the International North Pacific Fisheries Commission (INPFC), annual harvesting restrictions have been fashioned for Pacific ocean perch, *Sebastes alutus*, widow rockfish, *S. entomelas*, shortbelly rockfish, *S. jordani*, and thornyheads, *Sebastolobus* spp. The remaining rockfish species have been lumped into a single management unit, the *Sebastes* complex. In addition to individual trip limits, current restrictions for this large group involve an overall annual harvest guideline and harvest guidelines for two of its already stressed components, yellowtail, *Sebastes flavidus*, and canary, *S. pinniger*, rockfish (PFMC, 1992[1]). While efforts to prevent over-harvesting of yellowtail and canary rockfish continue, the fishing pressure on the minor rockfish in the management unit has escalated. Species, such as darkblotched rockfish, *S. crameri*, are becoming increasingly important to fishermen.

This research stems from a concern over the long-term effects of the trawl fishery on the condition of the rockfish community as a whole. Current reductions in some stocks along with present bycatch practices may precipitate the need for changes in management policies to conserve these stocks. One possible course of action involves multispecies management, whereby cooccurring species are managed as a species complex or assemblage. If needed, restrictions could be placed on the fishery for the assemblage when specific components become stressed. An effective assemblage management program requires knowledge of interspecific associations in addition to individual life histories, distribution, and abundance patterns.

Prior knowledge of offshore rockfish associations has largely been inferred from shoreside sampling of commercial catches. In recent years several investigations have been

[1] Pacific Fishery Management Council (PFMC). 1992. Status of the Pacific coast groundfish fishery through 1992 and recommended acceptable biological catches for 1993; stock assessment and fishery evaluation. Pacific Fishery Management Council, Metro Center, Suite 420, 2000 SW First Ave., Portland, OR 97201, 80 p.

conducted to identify assemblages using trawl data covering extensive geographic areas. Nagtegaal (1983) studied both annual and seasonal interrelationships of some rockfish species off British Columbia based on commercial catch data. However, these catch statistics do not allow a full description of the effects of selective harvest on the entire rockfish community, as the landed species are those of highest economic value allowed for harvest at the time and reflect only a portion of the overall rockfish community exposed to trawling. Rogers and Pikitch (1992) defined several groundfish assemblages based on prediscard data from the commercial trawl fishery off Oregon and Washington. That study included a variety of groundfish families, but only the most abundant rockfish species were considered. Similarly, Gabriel (1982) included a wide variety of groundfishes in a 1-year assemblage study that utilized 1977 survey data from California to Washington. All of these researchers recognized the value of fish assemblage identification as a tool for fisheries management and emphasized the need to verify assemblage persistence.

Since 1977, the Alaska Fisheries Science Center (AFSC) of the National Marine Fisheries Service (NMFS) has been conducting controlled bottom trawl surveys aimed at assessing and monitoring groundfish resources off the west coast of the United States. Now that several of these surveys have been performed, a unique opportunity exists to monitor persistence in fish assemblages. In this paper I describe and summarize these surveys and their rockfish samples and use standard numerical classification techniques to identify the major rockfish assemblages.

Methods

This study utilizes rockfish catch data from six AFSC multispecies groundfish assessment surveys conducted triennially over a 16-year period from 1977 to 1992. Only data from bottom trawling in the Columbia and U.S.-Vancouver INPFC areas (43°00'N to the U.S.-Canada border) were examined. Trawling occurred during August and September between the depths of 55 and 366 m. All surveys employed stratified random sampling designs, apportioning towing sites according to various geographic strata and depth intervals. While the overall multispecies assessment goal remained unchanged from one survey to the next, many of the specific objectives did not. Objectives of the 1977 survey included determining the distribution and abundance of several commercially important rockfishes (Gunderson and Sample, 1980) and the on-bottom component of Pacific hake, *Merluccius productus*. The survey design was patterned after rockfish distributions, determined by fisheries catch data and the results of a pilot rockfish survey (Gunderson and Nelson[2]). The 1980 survey was specifically redesigned to better assess the canary and yellowtail rockfish populations, in addition to Pacific hake (Coleman, 1986). Thus, the sampling effort was divided among three depth strata: 55–183 m, 184–220 m, and 221–366 m. The 1983 survey repeated the work conducted in 1980 with the addition of some stations in the northern U.S.-Vancouver area (Weinberg et al., 1984). Based on the results of the previous surveys and in an attempt to further reduce the variance of canary and yellowtail rockfish catch rates, station allocation was changed again in 1986 (Coleman, 1988). In that year, sampling was apportioned among four depth strata: 55–91 m, 92–183 m, 184–219 m, and 220–366 m. Almost three times the effort was applied in the U.S.-Vancouver area, most of which was off northern Washington (lat. 48°00'–42°23'N). However, having not been able to improve rockfish estimates significantly, the 1989 and 1992 AFSC surveys shifted away from rockfish concerns of past surveys and concentrated on abundance estimation of Pacific hake and young sablefish, *Anoplopoma fimbria*. Consequently, the high density rockfish strata were abandoned and sampling was allocated within only two depth strata, 55–183 m and 184–366 m (Weinberg et al., 1994).

Samples were collected with standardized Nor'eastern high-opening rockfish bottom trawls rigged with roller gear. In general the gear's horizontal and vertical openings measured 13 and 9 m, respectively. Towing was controlled by fishing along depth contours for one-half hour at about three knots. Catches were sorted by species, weighed, and counted.

Assemblage analyses

I examined rockfish associations using two techniques: recurrent group analysis and cluster analysis. These two methods provide somewhat different characterizations of species distribution and cooccurrence and, when used together, can enhance our understanding of rockfish communities.

Recurrent group analysis (RGA), a nonhierarchical technique, addresses the question of which rockfish are likely to be caught together, thus reflecting their

[2] Gunderson, D. R., and M. O. Nelson. 1977. Preliminary report on an experimental rockfish survey conducted off Monterey, California, and in Queen Charlotte Sound, British Columbia, during August-September 1976. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northwest and Alaska Fish. Cent., 2725 Montlake Blvd. E., Seattle, WA 98112. Unpubl. manuscr., 82 p.

spatial distribution patterns (Fager and McGowan, 1963). Species were included in a group based solely on their presence or absence in catches. Fixed groups were defined as the greatest number of members having affinities with one another based on a 40% affinity threshold.

However, because fishermen are concerned primarily with abundance in terms of biomass, the findings of RGA were supplemented by cluster analysis (CA), a method that incorporates sample catch weights into the grouping process. CA calculates resemblance measures using the Bray-Curtis dissimilarity coefficient (Bray and Curtis, 1957) and then clusters agglomeratively, using a flexible sort fusion strategy with an assigned clustering coefficient value (beta) equal to –0.25 (Lance and Williams, 1967). The flexible strategy was selected over other clustering methods because of its tendency to reduce the chaining effect often seen in dendrograms. Dendrograms display the similarities among species and groups in hierarchical form, permitting greater flexibility in the interpretation of associations than the RGA technique which produces set groups (Clifford and Stephenson, 1975). Relative groupings can be distinguished at varying levels of dissimilarity where the number 0 indicates greatest resemblance.

Prior to classifying assemblages, steps were taken to reduce "noise" in the data. First, groundfish species other than scorpaenids were eliminated, since the objective of the study was to identify rockfish assemblages without the masking effect caused by the presence of other species. Next, the least frequent rockfishes, defined as those taken at fewer than three stations in each of the groundfish surveys, were omitted. Knowledge of the path width of our survey gear facilitated the standardization of catch data as catch per unit of effort (CPUE), i.e. kilograms per hectare towed (kg/ha)[3], or roughly equivalent to towing our gear for 0.8 km. Finally, CPUE's were log transformed ($\log_{10}(x+1)$) to reduce the influence of high CPUE's (Boesch[4]).

Results

Over the six surveys, a total of 1,874 successful hauls were made in the Columbia and U.S.-Vancouver INPFC areas (Fig. 1). Rockfish were present in 79% (1,476) of the tows. Sampling effort was greatest in 1986 and considerably lower during 1977, 1989, and 1992. Most of the effort was applied between the depths of 101 and 200 m (Fig. 2). Sampling at greater depths was proportionally higher in 1977 than during the other surveys.

Catch composition and species diversity

Thirty three rockfish species (shortspine thornyhead *Sebastolobus alascanus* and 32 species of *Sebastes*) were identified. Among these, 20 were commonly caught in 1,468 hauls and included in the assemblage analysis (Table 1).

Catches of rockfish varied widely in size and composition. Many of the catches were small: 25% had CPUE's under 1.1 kg/ha and 50% had CPUE's under 4.8 kg/ha. In contrast, 8% were greater than 100 kg/ha while only 1% were greater than 500 kg/ha. Maximum rockfish CPUE's reached 4,126, 564, 1,253, 759, 2,303, and 828 kg/ha during the six respective surveys. The average CPUE for each survey was 50, 16, 34, 21, 34, and 27 kg/ha, respectively. On average, abundance levels increased in deeper water, peaking in the 151–250 m depth interval (Fig. 3).

Species diversity in survey catches depicts the multispecies nature of the rockfish community vulnerable to the bottom trawl. Eighty three percent of rockfish samples contained more than one species. Of these, approximately 50% contained 2–5 species, 29% contained 6–10 species, and 4% contained 10–16 species. Of the single-species catches, 78% were under 1 kg/ha. In contrast, the two largest single-species catches (canary rockfish) exceeded 100 kg/ha. Eighty five percent of the single-species samples were either shortspine thornyhead (7%), canary (26%), darkblotched (21%), yellowtail (18%), or green-striped, *Sebastes elongatus* (14%), rockfish. Silvergray, *S. brevispinis*, rosethorn, *S. helvomaculatus*, redbanded, *S. babcocki*, and yellowmouth, *S. reedi*, rockfish were never caught alone.

Species diversity, like abundance, increased with depth (Fig. 4). Hauls made at the shallowest sampling sites (~55 m) demonstrated little variety. As sampling depth increased, nearshore species, such as black, *S. melanops*, and quillback, *S. maliger*, rockfish, were replaced by offshore rockfishes, including juveniles of many species that inhabit even deeper waters as adults. Over the middle-shelf, within the 55–150 m depth interval, up to 13 rockfish species were taken in a single tow. About 22% of the hauls made at these depths contained five or more species (Table 2). Species diversity peaked along the outer-shelf, where the centers of abundance for several species overlapped. In waters 151–250 m deep, catches

[3] 1 kg/ha=0.1 t/km^2.

[4] Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. Virginia Inst. Marine Science, Spec. Sci. Rep. 77, EPA-600/3-77-033, 114 p. Environ. Res. Lab., Off. Res. Dev., U.S. Environ. Protection Agency, Corvallis, OR 97330.

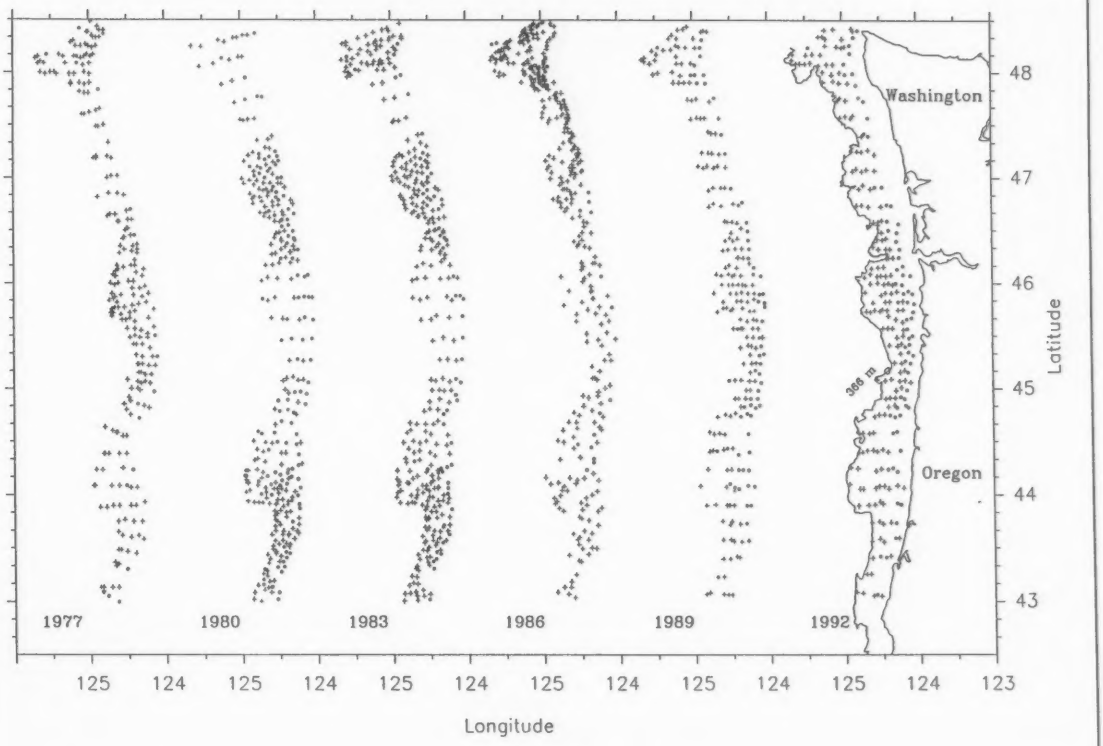


Figure 1

The distribution of hauls from the west coast triennial groundfish surveys showing the presence (+) or absence (o) of rockfish (Scorpaenidae) in the Columbia and U.S.-Vancouver areas.

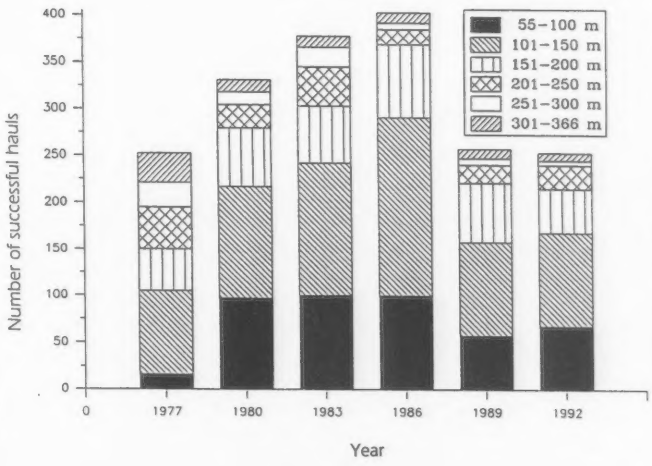


Figure 2

Distribution of successful survey effort by depth interval for the west coast triennial groundfish surveys (1977–92).

Table 1

The frequency of occurrence of rockfishes (Scorpaenidae) in the Columbia and U.S.-Vancouver areas from the west coast triennial groundfish surveys (1977–92).

Scientific name	Common name	Frequency of occurrence						
		1977	1980	1983	1986	1989	1992	Total
Species included in assemblage analyses								
Sebastolobus alascanus	Shortspine thornyhead	140	92	130	113	81	57	613
Sebastes aleutianus	Rougheye rockfish	39	19	36	54	47	46	241
Sebastes alutus	Pacific ocean perch	129	52	92	80	43	54	450
Sebastes babcocki	Redbanded rockfish	72	40	61	40	41	33	287
Sebastes brevispinis	Silvergray rockfish	31	23	54	34	11	8	161
Sebastes crameri	Darkblotched rockfish	129	99	172	163	128	105	796
Sebastes diploproa	Splitnose rockfish	90	38	90	56	50	33	357
Sebastes elongatus	Greenstriped rockfish	98	92	191	185	123	124	813
Sebastes entomelas	Widow rockfish	45	23	45	36	17	24	190
Sebastes flavidus	Yellowtail rockfish	90	83	153	130	44	53	553
Sebastes helvomaculatus	Rosethorn rockfish	42	36	64	59	46	48	295
Sebastes jordani	Shortbelly rockfish	5	46	39	28	11	5	134
Sebastes paucispinis	Bocaccio	45	36	60	34	10	3	188
Sebastes pinniger	Canary rockfish	74	68	143	155	63	50	553
Sebastes proriger	Redstripe rockfish	29	27	47	43	37	28	211
Sebastes reedi	Yellowmouth rockfish	6	4	11	6	4	8	39
Sebastes ruberrimus	Yelloweye rockfish	13	12	23	26	24	19	117
Sebastes saxicola	Stripetail rockfish	35	26	45	27	26	24	183
Sebastes wilsoni	Pygmy rockfish	3	7	21	20	27	13	91
Sebastes zacentrus	Sharpchin rockfish	74	39	82	77	53	48	373
Species excluded from assemblage analyses								
Sebastes aurora	Aurora rockfish	1	—	2	—	—	1	4
Sebastes borealis	Shortraker rockfish	5	1	3	2	—	—	11
Sebastes chlorostictus	Greenspotted rockfish	1	5	1	2	1	3	13
Sebastes eos	Pink rockfish	2	—	—	—	—	—	2
Sebastes goodei	Chilipepper	—	4	4	1	3	1	13
Sebastes levis	Cowcod	—	—	—	—	2	1	3
Sebastes maliger	Quillback rockfish	1	—	1	5	2	3	12
Sebastes melanops	Black rockfish	—	4	7	10	2	—	23
Sebastes melanostomus	Blackgill rockfish	—	4	1	—	—	—	5
Sebastes nigrocinctus	Tiger rockfish	—	—	1	—	—	—	1
Sebastes ovalis	Speckled rockfish	—	—	—	2	—	—	2
Sebastes rufus	Bank rockfish	—	—	1	—	1	1	3
Sebastes semicinctus	Halfbanded rockfish	—	—	—	—	2	—	2

contained up to 16 rockfish species; 73% of the samples contained five or more species. Samples ranging between 251–366 m in depth had up to 13 rockfish species with 52% of the samples having 5 or more species. Rockfish diversity declined at the deepest sites (~366 m).

Species assemblages

A total of 1,468 multispecies hauls were pooled together into a multi-survey, "All Years" analysis. Of the 20 rockfish species examined, 10 were identified as belonging to one of three groups or assemblages. Table 3 lists the results of RGA. The results of CA are shown in Figure 5 and summarized in Table 4. Group 1 consisted of shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish, *S. diploproa*. These four species occurred together in 200 samples at an average depth of 247 m (range=141–366 m). The mean rockfish CPUE in these hauls was 45.8 kg/ha of which the assemblage accounted for 82% of the total. Group 2 consisted of canary, yellowtail, and greenstriped rockfish. It also occurred in 200 survey hauls that averaged 150 m in depth (range= 91–291 m). Rockfish catches in hauls containing this assemblage were greater than Group 1, averaging 88.8 kg/ha. Canary, yellowtail, and greenstriped rockfish accounted for about 56% of the total rockfish CPUE at these sites. Group 3 consisted of sharpchin, redstripe, and rosethorn rockfish. This group was present in 99 samples. Its depth range

Table 2

Number of rockfish species (Scorpaenidae) from the west coast triennial groundfish surveys (1977–92) by depth interval in the Columbia and U.S.-Vancouver areas.

	Number of hauls per depth interval (m)						
Number of species	55–100	101–150	151–200	201–250	251–300	301–366	55–366
0	242	124	16	6	5	5	398
1	111	115	12	4	4	4	250
2	33	123	20	3	5	5	189
3	35	123	35	10	3	7	213
4	6	94	42	10	9	8	169
5	5	63	53	14	15	15	165
6	2	44	33	24	14	18	135
7	3	21	32	19	12	12	99
8	0	16	28	25	4	5	78
9	1	12	29	22	3	5	72
10	0	5	19	11	2	1	38
11	0	1	18	13	1	0	33
12	1	0	8	5	1	0	15
13	0	1	8	2	2	0	13
14	0	0	1	1	0	0	2
15	0	0	1	3	0	0	4
16	0	0	1	0	0	0	1
Total	439	742	356	172	80	85	1874

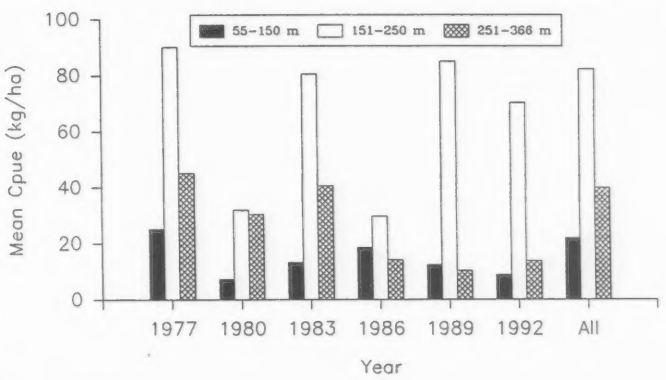


Figure 3

Relative abundance of rockfish (Scorpaenidae) expressed as mean catch per unit of effort (CPUE) for selected depth intervals by survey and for all surveys combined.

overlapped that of Group 2, 99–293 m, but this group was present, on average, in slightly deeper waters, 175 m (Fig. 6). Catches of this assemblage seemed to be more localized than were the others, occurring mainly in areas of highly irregular or hard bottom. Catch rates were highest at sites where this assemblage was present, averaging 159 kg/ha of which these three species accounted for 79% of the total. Shortbelly and pygmy rockfish, *S. wilsoni*, were also grouped together based on very low occurrences, probably an artifact of the grouping process.

The groupings assigned by the RGA and CA techniques were indentical except for two species. These were the assignment of redbanded rockfish to Group 1 by RGA only; and the assignment of greenstriped rockfish to Group 3 by RGA and Group 2 by CA.

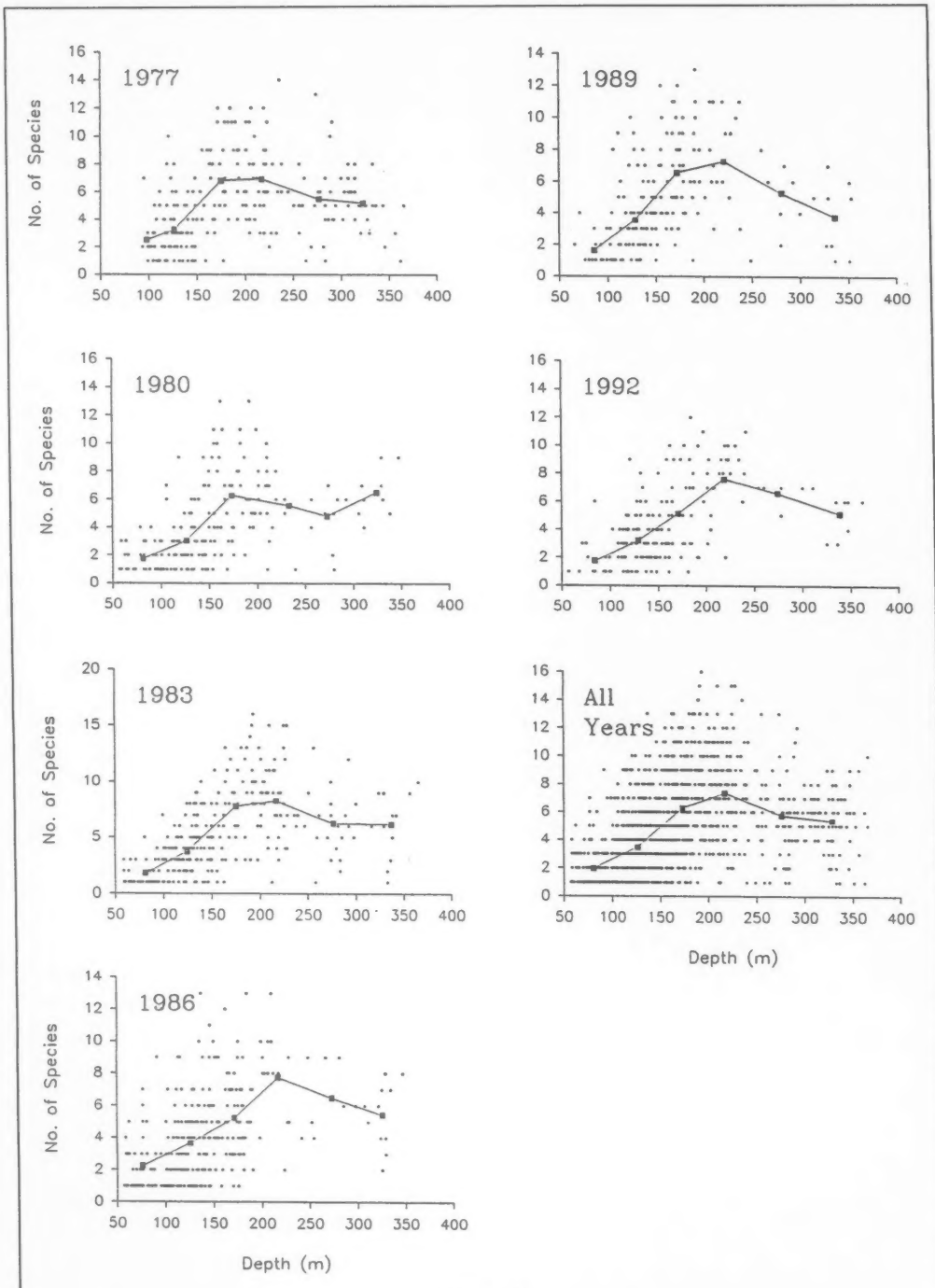


Figure 4

Number of rockfish species (Scorpaenidae) per tow (dots) and averaged over 55–100, 101–150, 151–200, 201–250, 251–300, and 301–366 m depth intervals (squares).

Table 3

Major species groups (1–3) of rockfish (Scorpaenidae) determined by recurrent group analysis by survey and for all surveys combined. Depth (m) and catch per unit of effort (CPUE, kg/ha) statistics refer to samples when all species listed in the group cooccurred. The group mean catch is also presented as the percent of the total average rockfish catch in those hauls. See Table 1 for scientific names.

Species	1977	1980	1983	1986	1989	1992	All years
Shortspine thornyhead	1	1	1	1	1	1	1
Pacific ocean perch	1	1	1	1	—	1	1
Splitnose rockfish	1	1	1	1	1	1	1
Darkblotched rockfish	1	—	1	1	1	2	1
Redbanded rockfish	1	1	—	—	1	1	1
Canary rockfish	2	2	2	2	3	—	2
Yellowtail rockfish	2	—	2	2	—	2	2
Greenstriped rockfish	2	2	1	3	3	2	3
Sharpchin rockfish	3	3	3	3	3	3	3
Rosethorn rockfish	3	3	3	3	3	3	3
Redstripe rockfish	—	—	3	—	—	3	3

Depth and catch statistics	Group 1	Group 2	Group 3
1977			
Occurrences	41	34	31
Mean depth (range)	255 (155–344)	163 (104–291)	217 (108–315)
Mean group CPUE (range)	48.7 (6.2–496.0)	57.6 (1.3–599.4)	11.2 (0.2–72.4)
Proportion of total CPUE (%)	79.8	63.5	9.5
1980			
Occurrences	19	37	24
Mean depth (range)	249 (150–338)	154 (82–274)	195 (144–348)
Mean group CPUE (range)	39.7 (0.9–155.7)	14.0 (0.2–116.7)	11.2 (0.1–94.4)
Proportion of total CPUE (%)	73.6	23.6	13.1
1983			
Occurrences	31	80	26
Mean depth (range)	213 (154–293)	143 (59–251)	196 (124–293)
Mean group CPUE (range)	32.2 (1.7–126.0)	36.1 (0.6–742.5)	71.1 (0.1–681.8)
Proportion of total CPUE (%)	67.9	47.1	34.5
1986			
Occurrences	31	73	34
Mean depth (range)	233 (150–348)	124 (59–185)	165 (97–267)
Mean group CPUE (range)	37.3 (1.5–417.8)	48.0 (0.1–745.3)	9.2 (0.3–87.4)
Proportion of total CPUE (%)	89.2	79.7	15.8
1989			
Occurrences	27	—	22
Mean depth (range)	230 (132–353)	—	174 (112–238)
Mean group CPUE (range)	9.8 (0.3–64.8)	—	22.7 (0.6–92.4)
Proportion of total CPUE (%)	36.3	—	23.3
1992			
Occurrences	9	24	15
Mean depth (range)	230 (214–260)	155 (119–219)	167 (113–223)
Mean group CPUE (range)	31.0 (7.9–98.8)	25.6 (1.3–283.3)	120.8 (0.7–533.4)
Proportion of total CPUE (%)	53.5	76.2	67.3
All years			
Occurrences	135	278	89
Mean depth (range)	259 (155–366)	141 (59–291)	173 (97–293)
Mean group CPUE (range)	45.9 (1.7–496.0)	53.3 (0.1–1205.2)	26.1 (0.3–684.7)
Proportion of total CPUE (%)	80.3	62.8	12.5

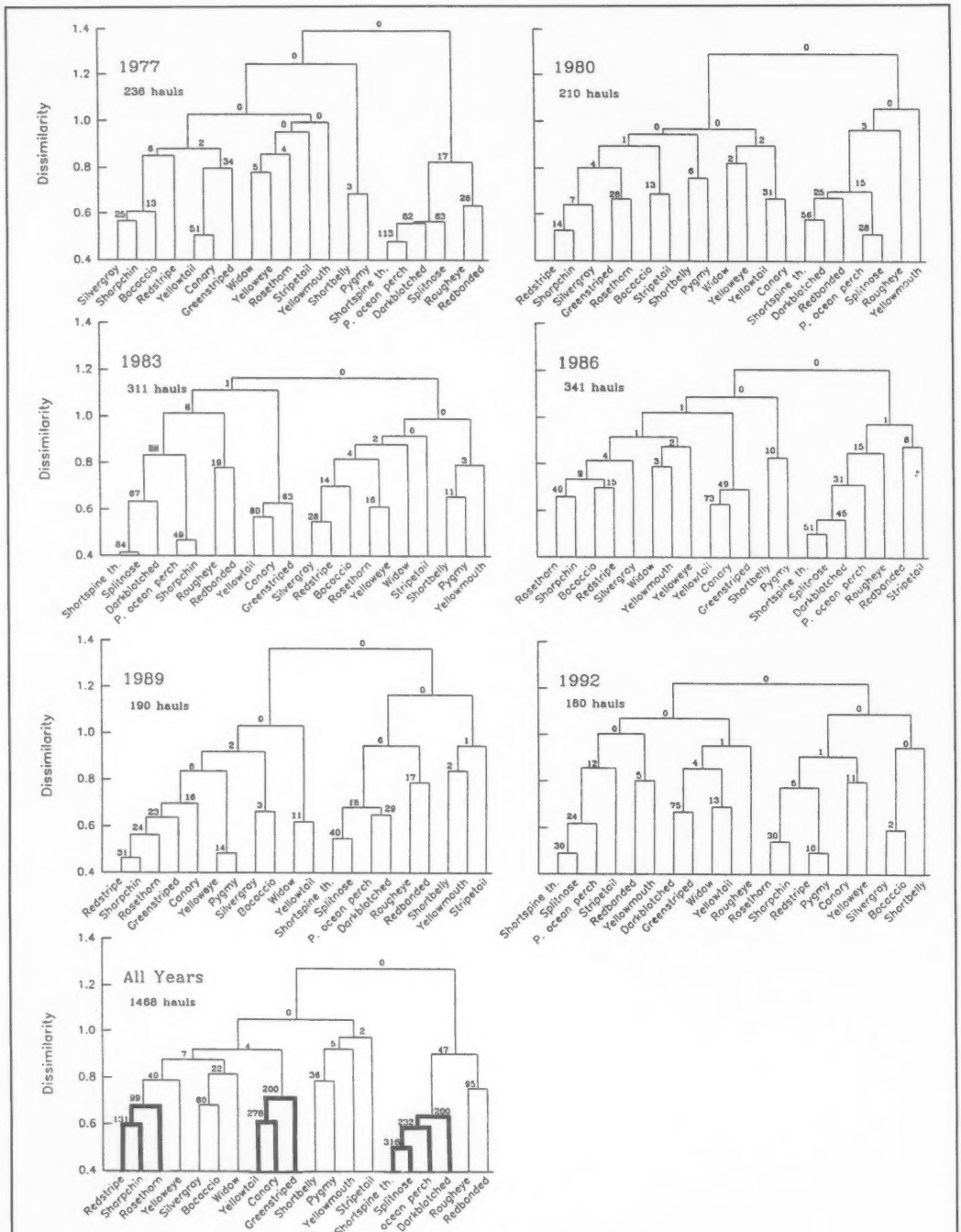


Figure 5

Dendrograms showing the relationships among rockfish (Scorpaenidae) species and assemblages (in bold) in the Columbia and U.S.-Vancouver areas. The values on top of each cluster correspond to its frequency of occurrence with all members present.

Table 4

Catch per unit of effort (CPUE) and depth (m) data from the combined 1977–92 west coast triennial groundfish surveys presented for the three rockfish (Scorpaenidae) assemblages identified by cluster analysis. The species catch composition data (listed across) are from hauls containing these assemblages and include mean CPUE (kg/ha) and standard deviation; the percentage of the total rockfish CPUE taken in these hauls, and the percent frequency of occurrence. Values below 0.1 are indicated by the letter *t*. Differences in totals are a result of rounding. See Table 1 for scientific names.

All years (1977–92)	Group 1				Group 2				Group 3			
Total hauls[1]	200				200				99			
Mean depth (range)	247 (141–366)				150 (91–291)				175 (99–293)			
Mean CPUE	45.8				88.8				158.6			
Catch composition	Mean CPUE	SD	% CPUE	% Occur.	Mean CPUE	SD	% CPUE	% Occur.	Mean CPUE	SD	% CPUE	% Occur.
Group 1												
Darkblotched	9.0	2.26	19.7	100.0	1.4	0.27	1.6	52.0	0.5	0.22	0.3	22.2
Pacific ocean perch	17.6	3.06	38.4	100.0	2.9	1.03	3.4	26.0	9.6	3.14	6.1	53.5
Shortspine thornyhead	3.8	0.29	8.4	100.0	0.5	0.13	0.5	37.5	0.7	0.16	0.4	46.4
Splitnose	7.0	1.03	15.4	100.0	0.3	0.10	0.3	21.0	1.1	0.42	0.7	26.3
Total	37.4		81.9		5.2		5.8		12.0		7.5	
Group 2												
Canary	0.4	0.14	0.9	25.5	15.4	4.03	17.3	100.0	16.8	5.59	10.6	66.7
Greenstriped	0.6	*t*	1.3	48.0	2.7	0.33	3.0	100.0	3.9	0.59	2.4	89.9
Yellowtail	0.6	0.19	1.3	19.0	31.2	6.18	35.1	100.0	24.3	7.39	15.3	50.5
Total	1.6		3.5		49.2		55.5		44.9		28.3	
Group 3												
Redstripe	*t*	*t*	0.2	8.0	14.1	4.10	15.9	33.5	46.1	10.28	29.1	100.0
Rosethorn	0.2	*t*	0.4	34.0	0.6	0.14	0.7	40.5	1.9	0.26	1.2	100.0
Sharpchin	3.0	0.78	6.7	43.5	9.8	3.91	11.1	39.5	31.1	8.36	19.6	100.0
Total	3.2		7.3		24.5		27.6		79.1		49.9	
Other rockfish												
Bocaccio	0.3	*t*	0.6	16.5	1.5	0.34	1.7	37.0	2.5	0.68	1.6	42.4
Pygmy	*t*	*t*	*t*	3.0	0.5	0.27	0.6	14.0	3.4	1.52	2.2	31.3
Redbanded	0.8	0.12	1.7	67.5	0.6	0.29	0.7	14.0	0.4	0.16	0.3	28.3
Rougheye	0.5	0.12	1.1	31.5	0.2	*t*	0.2	9.5	*t*	*t*	*t*	7.1
Shortbelly	*t*	*t*	0.2	8.5	0.3	0.14	0.3	18.5	0.7	0.34	0.4	24.2
Silvergray	0.4	0.20	0.9	10.5	1.6	0.38	1.9	25.5	8.8	5.18	5.5	45.4
Stripetail	0.3	*t*	0.7	31.0	0.3	*t*	0.3	17.0	0.5	0.17	0.3	31.3
Widow	0.4	0.19	0.9	23.5	3.4	1.66	3.9	25.5	3.1	1.73	2.0	27.3
Yelloweye	*t*	*t*	0.2	3.0	1.1	0.39	1.2	20.0	1.7	0.69	1.1	40.4
Yellowmouth	*t*	*t*	0.2	3.5	0.1	*t*	0.1	4.0	1.1	0.49	0.7	16.2
Remaining rockfish	0.4		0.5		0.2		0.2		0.3		0.2	
Total	3.4		7.2		9.8		11.1		22.5		14.3	

[1] Includes 18 hauls having both Groups 1 and 2; 11 hauls having both Groups 1 and 3; and 36 hauls having both Groups 2 and 3.

In addition to the "All Years" analysis, individual surveys were classified, revealing moderate agreement among surveys. Of the two methods, RGA (presence-absence) produced more consistent results across individual surveys. Changes in the structure of the three assemblages in any given year usually involved the addition or omission of one species or the shifting of one of the more ubiquitous species into another group.

On the other hand, assemblage patterns across surveys were less discernible with the biomass-oriented CA because of the high variability in rockfish CPUE's, particularly among shelf species. Usually, at the highest dissimilarity level (Fig. 5), CA partitioned the offshore community into a deep water, upper-slope group and a shallower water, mid-shelf group. The deeper species consisted of shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish. Two additional species, redbanded and rougheye, *S. aleutianus*, rockfish, were often closely associated with this group. In 1983, sharpchin, *S. zacentrus*, rockfish was included. The shallower species comprised two core assemblages (most easily seen in the "All Years" dendrogram). The first of these consisted of canary, yellowtail, and to a lesser extent, greenstriped rockfish. This assemblage was clearly identified from 1977 through 1986. However, in 1989 and 1992, it was not defined, most likely because of the shift in survey design that de-emphasized canary and yellowtail rockfish as target species, thus reducing the sampling effort in areas where they were most likely to have been found together. The other core assemblage among shelf rockfishes consisted of sharpchin, rosethorn, and redstripe rockfish, *S. proriger*. However, since these species were taken along with a variety of other species, such as silvergray rockfish, bocaccio, *S. paucispinis*, yelloweye, *S. ruberrimus*, canary, and yellowtail rockfish, CA dendrograms showed considerable variability between years.

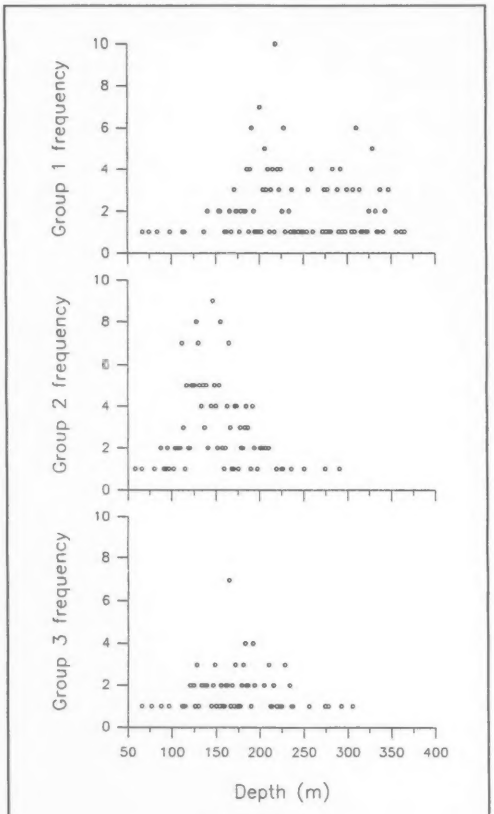


Figure 6

The frequency of occurrence by depth of the three rockfish assemblages determined from cluster analysis. Group 1 consists of shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish. Group 2 consists of yellowtail, canary, and greenstriped rockfish. Group 3 consists of sharpchin, redstripe, and rosethorn rockfish. See Table 1 for scientific names.

Discussion

Survey data have provided the unique opportunity to study broad-scale community composition of offshore rockfishes, including smaller specimens typically discarded in commercial operations. These data are useful to both ecologists interested in describing the biological associations of our ocean's resources and to resource managers concerned with commercial catch and bycatch issues.

For a variety of reasons however, survey-defined assemblages may differ from assemblages determined through commercial fisheries data. Most of these revolve around the strict adherence to scientific design of most surveys as opposed to industry's opportunistic approach driven by economic needs. For example, the assemblages identified in this study would probably not be detected if sampling were limited to catches made while targeting strong hydroacoustic signals (Richards et al., 1991). Pelagic and semipelagic aggregations, such as widow, shortbelly, and in some cases yellowtail rockfish are under-represented in this study because they were sampled less intensively during the surveys. Differences in catch composition is also gear dependent. Our survey gear and methods of deployment were standard-

ized to facilitate comparisons among surveys. The trawl employed a 89-mm mesh codend with a 32-mm liner, capable of retaining juveniles and smaller-sized species, such as rosethorn and greenstriped rockfish. Smaller species may not be caught in similar proportions in commercial catches.

On the other hand, fishermen select, modify, and operate their gear based on fishing strategy. These strategies have changed over the years to adapt to reduced allowable harvests and the imposed vessel trip limits. To economize, fishermen target several species over the course of a single trip, using more than one type of gear (Tagart[5]). For example, a vessel may begin using midwater gear directed at catching a limit of widow rockfish, then switch to bottom gear to target on yellowtail rockfish. Once the trip limits for these two species are reached, the captain may opt to fish flatfish or change to a more generalized rockfish strategy keeping larger specimens of darkblotched, silvergray, redstripe, or sharpchin rockfish.

Because survey and fishery tactics differ greatly, I assessed whether the assemblages found to persist in summer surveys based on systematic sampling also occurred in commercial collections characterized by opportunistic sampling, market conditions, and management-imposed restrictions. The literature referred to previously describes various west coast fish assemblages determined from different sampling techniques, classification methods, and data types. Although none of these studies used a time-series of this duration, Rogers and Pikitch (1992) identified two rockfish assemblages using year-round (1985–87), prediscard, commercial trawl data from off the coasts of Oregon and Washington. Briefly, they examined five fishing strategies, one of which targeted demersal rockfishes using bottom trawl gear. Even though the survey depth range was narrower than that of the commercial operations, the results of Rogers and Pikitch (1992) share much in common with the present study. Both studies describe an assemblage of deepwater rockfishes with three species in common: Pacific ocean perch, darkblotched rockfish, and splitnose rockfish. The present study also includes shortspine thornyhead, whereas Roger and Pikitch (1992) include sharpchin and yellowmouth rockfish.[6] Their second rockfish assemblage combined bocaccio, yellowtail, canary, yelloweye, and sharpchin rockfish, species assigned to either one of two separate assemblages or caught too inconsistently to be considered part of any assemblage in the present study.

Rogers and Pikitch (1992) included in their analysis 11 of the 20 scorpaenids that I examined. These were selected based on either an arbitrarily determined weight threshold (1% of the total commercial catch from all five fishing strategies) or if fishermen claimed to target a species (e.g. bocaccio and yelloweye rockfish). Most of those selected represented larger proportions of the commercial catch; however, other rockfishes were continuously affected by trawling. When classifying assembages based on biomass data, one takes the risk of failing to recognize a less abundant member of the community. In the study by Rogers and Pikitch (1992), several minor rockfish species were overshadowed by catches of the area's dominant species. Nearly 60% of the total catch sampled from all fishing strategies combined was nonrockfish. Among the rockfishes, widow rockfish accounted for the highest percentage (15%) of the sample catch, about 75% of which was taken by midwater trawl (Rogers[7]). Assuming that the data from their study is representative of commercial operations, we can infer the impact that trawling has on the overall rockfish community, including the minor species, by examining prediscard catch data from hauls where bottom rockfish were targeted (i.e. bottom rockfish fishing strategy). In these data, nonrockfish composed only 20% of the catch whereas widow rockfish, taken by bottom trawl, still accounted for 15% of the strategy's total. Of the species assemblages identified in the present study, yellowtail, canary, and greenstriped rockfish accounted for 30% of the total; shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish accounted for 13%; and sharpchin, redstripe, and rosethorn rockfish accounted for 10% of the total catch. Large marketable species typically seen in the landings, like bocaccio, silvergray rockfish, and yelloweye rockfish, composed only 4% of the prediscard catch.

Conclusion

The separation of deepwater species from shelf species supports the division of the "*Sebastes* complex" management category into smaller units of greater ecological consequence, as also suggested by Rogers and Pikitch (1992). There is enough variability, however, in the catches of shelf rockfish, as characterized by the relatively high levels of dissimilarity among groupings (Fig. 5), to warrant the use of caution when designating assemblages. While this study recognized two assemblages of shelf species vulner-

[5] Tagart, J. Washington Dept. Fish., Olympia, WA 98504-3144. Personal commun., April 1991.

[6] For unknown reasons, fishery data had substantially greater abundance of yellowmouth rockfish than did the survey data.

[7] Rogers, J. B. Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Tiburon, CA 94920. Personal commun., Nov. 1993.

able to bottom trawling off Oregon and Washington, a resource manager may elect to base management decisions on the union of these two because of the difficulty in monitoring the often discarded sharpchin-redstripe-rosethorn rockfish assemblage. However, in managing the rockfish community as a whole, this assemblage needs to be considered along with other minor species commonly caught in the fishery.

Our understanding of the associations among rockfish has improved greatly. Assemblage studies, combined with studies on life history, distribution, and abundance, continue to assist in refining current resource management policies and may eventually lead to a more multispecies management approach. Such an approach will address the impact on the ecosystem when operations target on a single species, such as yellowtail rockfish, with little regard to the effects on other species, particularly those of lower economic value. Likewise, it will also address the continued removal of a species like yellowtail rockfish due to incidental catch when operations target on another species.

Acknowledgments

Fisheries biologists must often endure the harsh marine environment for extended periods of time, forsaking the more comfortable conditions of their offices and homes. I thank all of the participants, scientists, and crews of the NMFS west coast triennial surveys. Gary Walters was responsible for bringing the cluster analysis program to the AFSC and provided guidance for its use. Mark Wilkins realized this study's benefits and enabled my escape from many routine exercises to complete this work. I am also most grateful to my reviewers, particularly those who witnessed the evolution of this paper.

Literature cited

Bray, J. R., and J. T. Curtis.
1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

Clifford, H. T., and W. Stephenson.
1975. An introduction to numerical classification. Academic Press, Inc., NY, 229 p.

Coleman, B. A.
1986. The 1980 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, length and age composition. NOAA Tech. Memo. NMFS-F/NWC–100, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 181 p.

Coleman, B. A.
1988. The 1986 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, length and age composition. NOAA Tech. Memo. NMFS-F/NWC-152, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 145 p.

Eschmeyer, W. N., and E. S. Herald.
1983. A field guide to Pacific coast fishes of North America. Houghton Mifflin, Boston, 336 p.

Fager, E. W., and J. A. McGowan.
1963. Zooplankton species groups in the North Pacific. Science 140:453–460.

Gabriel, W. L.
1982. Structure and dynamics of northeastern Pacific demersal fish assemblages. Ph.D. diss., Oregon State Univ., Corvallis, 298 p.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3–4):2–16.

Lance, G. N., and W. T. Williams.
1967. A general theory of classificatory sorting strategies. I: Hierarchical systems. Comput. J. 1:15–20.

Nagtegaal, D. A.
1983. Identification and description of assemblages of some commercially important rockfishes (*Sebastes* spp.) off British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. Vol. 1, 82 p.

Richards, L. J., R. Kieser, T. J. Mulligan, and J. R. Candy.
1991. Classification of fish assemblages based on echo integration surveys. Can. J. Fish. Aquat. Sci. 48:1264–1272.

Rogers, J. B., and E. K. Pikitch.
1992. Numerical definition of groundfish assemblages caught off the coasts of Oregon and Washington using commercial fishing strategies. Can. J. Fish. Aquat. Sci. 49:2648–2656.

Weinberg, K. L., M. E. Wilkins, and T. A. Dark.
1984. The 1983 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, age and length composition. NOAA Tech Memo. NMFS-F/NWC-70, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 376 p.

Weinberg, K. L., M. E. Wilkins, R. R. Lauth, and P. A. Raymore Jr.
1994. The 1989 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, and length and age composition. NOAA Tech Memo. NMFS-AFSC-33, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 168 p.

Results of long-term, seasonal sampling for *Penaeus* postlarvae at Breach Inlet, South Carolina

Lawrence B. DeLancey
James E. Jenkins
J. David Whitaker
South Carolina Wildlife and Marine Resources Department
P.O. Box 12559, Charleston, South Carolina 29412

Recruitment of postlarvae of commercially important penaeid shrimp has been studied in several areas in the southeastern United States, e.g. on the Atlantic coast (Bearden, 1961; Williams and Deubler, 1968; Williams, 1969; Allen et al., 1980) and the Gulf of Mexico (Baxter, 1963; George, 1962; Loesch, 1965; Christmas et al., 1966; Baxter and Renfro, 1967; Caillouet et al., 1968, 1970; Ford and St. Amant, 1971). Findings from these studies indicate that postlarvae are generally concentrated near oceanic inlets, different species are abundant at different times of the year, ingress through inlets into estuarine nursery areas is often influenced by factors such as tide and time of day, and correlations between number of postlarvae and subsequent commercial landings is often poor.

In South Carolina most published studies have examined postlarval recruitment over a one- to two-year period (Bearden, 1961; Olmi, 1986; Wenner and Beatty, 1993). Long-term sampling was conducted by Lunz[1] at several coastal sites in South Carolina in an effort to predict subsequent commercial harvest. As an extension of this work, long-term, seasonal sampling was conducted at a single site near Charleston, South Carolina, to determine relative abundance and timing of recruitment of *Penaeus* postlarvae. This study is part of a continuing effort to relate postlarval abundance to subsequent landings and to evaluate spawning success of parental stocks.

Materials and methods

Samples were collected with a 1-m diameter, 500-µm mesh plankton net fitted with a flowmeter at Breach Inlet, South Carolina (between Sullivan's Island and the Isle of Palms), from January 1975 to August 1992 (Fig. 1). Breach Inlet is an oceanic inlet with high velocity tidal currents (up to 150 cm/sec flow). The tides in South Carolina are semidiurnal and have an average range of tidal height of approximately 2 m between mean low water and mean high water. Breach Inlet was chosen as a site for intensive monitoring of recruitment because of its accessibility (boats are not required for sampling and it can be sampled in inclement weather). Preliminary studies have shown that postlarvae can be collected in consistently high numbers (several hundred per sample) at Breach Inlet, and catches are comparable to collections made in other estuaries in South Carolina (J. Whitaker, unpubl. data).

The net was deployed from a bridge over the inlet and fished near the bottom (approx. 10 m depth) for two one-hour periods during daylight flood tides. Prior to 1978, paired samples were taken twice weekly (approximately 30 minutes elapsed between samples). This effort was greatly reduced when abundance of postlarval brown shrimp, *Penaeus aztecus*, could not be correlated with commercial landings. After 1977, regular sampling involved collecting two unpaired samples per tide at one or two week intervals from late January to early August. Hydrographic information, including water temperature and salinity, were also collected during sampling (Table 1).

In addition to bottom daylight samples, consecutive samples were taken over a full tidal cycle during day and night (two surface and two bottom samples per tide) in some years during periods of high abundance to examine possible influences of tide, time of day, and location of the net on postlarval catch rates. Consecutive samples of *P. aztecus* were collected on 12–13 March 1975, 26–27 February and 30–31 March 1976, 17–18 March 1977, 24–25 February and 10–11 March 1983, 2–3 March and 2–3 April 1985, and 21 February and 3–4 March 1986 (flood tide only in 1986). Consecutive samples for *P. setiferus* were collected on 9–10 June and 16–17 July 1975, 27–28 May and 28–29 June 1976, 9–10 June 1983, and 29–30 May 1989 (flood tide only in 1989).

Plankton samples were preserved in 10% buffered formalin-seawater and sorted in the laboratory. Postlarvae were sorted to species in most instances by using characteristics identified by Pearson (1939), Williams (1959), and

Contribution 335 of the South Carolina Marine Resources Center.

[1] Lunz, G. R. 1965. Annual report 1963–64, Bears Bluff Laboratories. Contrib. Bears Bluff Lab. No. 41, 10 p.

Manuscript accepted 6 January 1994.
Fishery Bulletin 92:633–640 (1994).

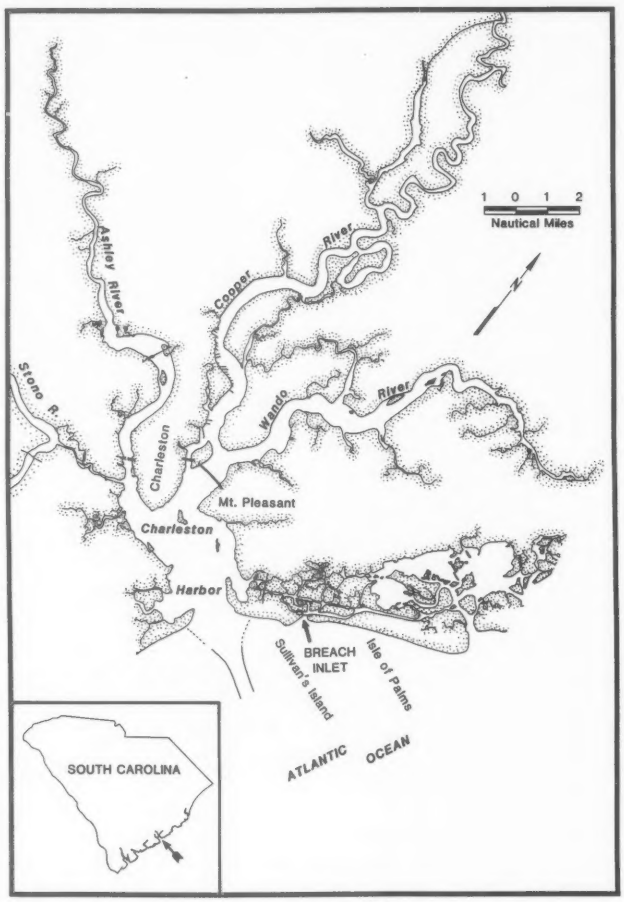


Figure 1

Map of Breach Inlet, South Carolina, site of collection of postlarval *Penaeus*.

Ringo and Zamora (1968). Postlarvae with overlapping characters were identified to genus.

Counts of postlarvae were converted to density (numbers per 1,000 m^3). Preliminary analyses revealed these data to be nonnormal and with large variation; therefore, potential effects of time of day, tidal stage, and location of nets (surface versus bottom) on ingress of postlarvae collected by consecutive sampling were tested with the nonparametric Mann-Whitney test on densities of postlarvae (flood tide only for time of day and location of nets; Siegel, 1956). The effect of lunar phase on catches made during regular sampling (daytime bottom collections made on flood tide during season of peak abundance) was tested with the nonparametric Kruskal-Wallis test on densities grouped by four lunar periods (new, full, first, or last quarter) pooled from the entire year's data (Siegel, 1956). Differences among groups were considered statistically significant at the $P \leq 0.05$ level. The above data were log-transformed to facilitate graphic representation of means and standard deviations (Figs. 2 and 3). An annual index of abundance ($\Sigma \log((\text{number}/1{,}000 m^3) + 1)/\text{number of samples}$); Elliot, 1977) was calculated for each species for use in regression analysis. The index was computed from February, once densities reached 20/1,000 m^3, through April for *P. aztecus*, and from May through August for *P. setiferus*. Annual indices of postlarval abundance were regressed against annual estimates of harvest to ascertain possible relation-

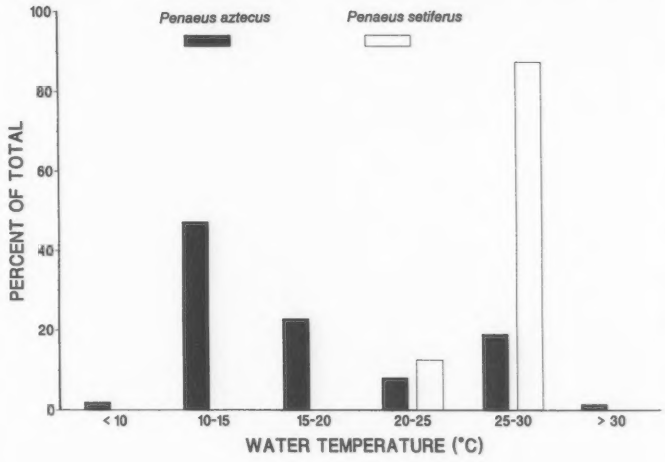


Figure 2

Distribution of catch of postlarval penaeid shrimp, *Penaeus aztecus* and *Penaeus setiferus*, over the range of water temperature observed at Breach Inlet during regular sampling.

ships.[2] Numbers of shrimp landed each year were estimated by multiplying landed weight by average grade (average number of shrimp per kg).

Results

A total of 102,109 *Penaeus* postlarvae were collected from 7 January 1975 to 3 August 1992 at Breach Inlet. Of the total catch, 68.3% were identified as brown shrimp, *P. aztecus*, 23.3% as white shrimp, *P. setiferus*, and 0.8% as pink shrimp, *P. duorarum*. The remaining 7.6% were identifed as *Penaeus* spp. The majority of the latter category were tentatively identified as *P. aztecus*, and were collected primarily from late May through July. Because *P. duorarum* postlarvae were collected in relatively low numbers and some uncertainty exists with identification, the analysis includes only *P.aztecus* and *P. setiferus*.

The majority of *P. aztecus* postlarvae were collected between February and April, when water temperature was between 10 and 20°C (the catch peaked between 12° and 16°C). *Penaeus setiferus* was collected only when temperatures exceeded 20°C; most were taken at temperatures between 25 and 30°C (peak abundance occurred in June; Fig. 2). Samples of *P. aztecus* averaged several hundred individuals in each year during times of peak ingress. However, catches of *P. setiferus* were much more variable, averaging zero in some years and several hundred in years of high abundance (Table 2).

Consecutive sampling conducted day and night on both ebb and flood tides revealed that both species

Table 1

Average and range of bottom water temperature and salinity observed at Breach Inlet, South Carolina and number of samples of *Penaeus* postlarvae collected during regular sampling, 1975–92.

Year	Temperature (°C)	Salinity (ppt)	Number of samples
1975	20.2 (9.3–29.4)	28.6 (15.0–35.0)	256
1976	19.4 (7.0–30.0)	30.7 (26.0–35.0)	236
1977	21.4 (4.9–32.1)	31.5 (21.0–36.0)	244
1978	21.2 (5.9–31.5)	29.8 (18.0–35.0)	117
1979	18.8 (6.7–28.2)	28.8 (24.0–35.0)	57
1980	15.3 (5.7–25.6)	28.8 (20.0–34.0)	34
1981	18.3 (10.9–31.0)	32.4 (25.0–36.0)	46
1982	18.9 (9.5–28.1)	28.5 (22.0–32.0)	22
1983	14.9 (8.1–26.2)	27.6 (18.0–32.0)	33
1984	23.7 (8.1–30.5)	29.0 (23.0–34.0)	63
1985	21.8 (11.3–30.7)	31.7 (26.0–36.0)	48
1986	20.8 (9.1–30.0)	31.1 (27.0–34.0)	36
1987	17.4 (8.0–29.2)	32.1 (26.0–36.0)	36
1988	19.4 (11.2–30.5)	29.1 (21.0–35.0)	38
1989	20.8 (10.5–30.6)	32.7 (26.0–36.0)	48
1990	21.3 (11.9–30.1)	31.1 (25.0–35.0)	42
1991	20.2 (10.4–29.4)	29.4 (21.0–35.0)	36
1992	21.3 (9.3–30.1)	29.1 (24.0–33.0)	34

[2] Low, R. A. 1992. Survey of the South Carolina Shrimp baiting fishery, 1991. South Carolina Marine Res. Cent. Data Rep. 9, 29 p.

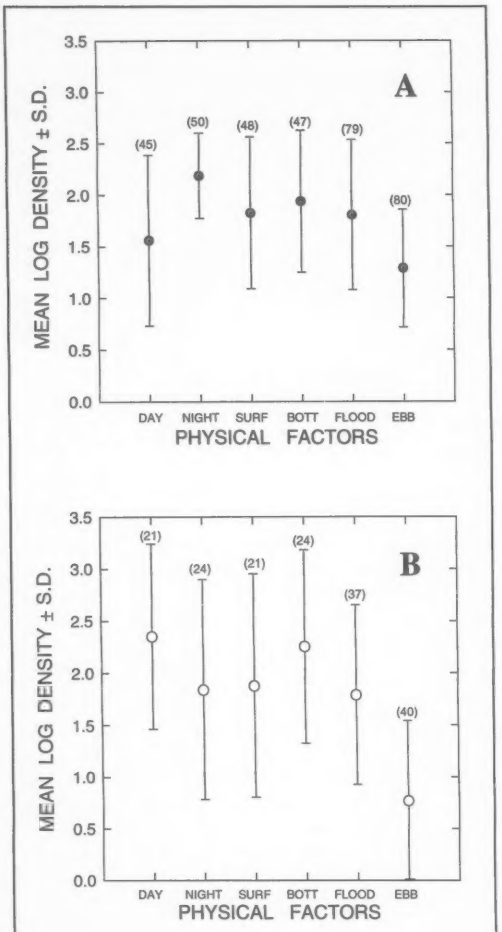


Figure 3

Mean density of postlarval penaeid shrimp (**A**) *Penaeus aztecus* and (**B**) *Penaeus setiferus* grouped by time of day, tide, and location of net at Breach Inlet, South Carolina. Samples were collected over 24-hour periods during times of peak abundance. Log Density= log((number/1,000m^3) + 1). SD=standard deviation. Numbers in parenthesis=number of samples. Surf=surface, Bott=bottom.

were significantly more abundant in samples taken during flood tides than during ebb tides (P<0.001; Fig. 3). Significantly more *P. aztecus* were collected at night on flood tides ($\bar{x}$=228.7/1,000m^3) than during daylight flood tides ($\bar{x}$=147.4/1,000m^3; P<0.001), whereas no significant difference between catches made during day ($\bar{x}$=877.9/1,000m^3) versus night ($\bar{x}$=610.2/1,000m^3) were noted for *P. setiferus* (P=0.114; Fig. 3). No significant differences in catches were noted for either species when surface and bottom collections were compared (P=0.595 for *P. aztecus*; P=0.270 for *P. setiferus*; Fig. 3).

Significant differences among catches made by regular sampling grouped by lunar phase (new moon, first quarter, full moon, last quarter) were detected for both *P. aztecus* (P<0.0001) and *P. setiferus* (P<0.006). Fewest postlarvae of both species were collected during full moon phases; *P. aztecus* were more abundant during the last quarter than at other times (Fig. 4), whereas *P. setiferus* was most abundant during the first quarter.

Results of correlation analysis revealed a low correlation (r^2=0.03; P=0.523) between annual indices of abundance of postlarval *P. aztecus* and subsequent landings. A much higher correlation was obtained for *P. setiferus* (r^2=0.79; P<0.001; Fig. 5). The regression equation for estimated number of *P. setiferus* landed was $Y = 40.4 + 119.0X$ (Y=estimated number landed, X=annual index of postlarval abundance).

Discussion

Our results are generally similar to observations on *Penaeus* postlarvae made by others in the southeastern United States (including the Gulf of Mexico). *Penaeus aztecus* is most abundant in springtime at water temperatures comparable to the range of temperatures observed in this study (Bearden, 1961; Williams and Deubler, 1968; Allen et al., 1980). It has been postulated that the majority of brown shrimp postlarvae recruited in the spring are produced by spawning from the previous fall (Temple and Fischer, 1967; Aldrich et al., 1968; Anderson, 1970; Whitaker[3]). Ingress begins after nearshore water temperatures approach 12°C. In contrast, *Penaeus setiferus* postlarvae are recruited in spring and summer shortly after being spawned in adjacent oceanic waters (Pearson, 1939; Lindner and Anderson, 1956). When compared to overall catches of *P. setiferus*, *P. aztecus* have often been collected in greater abundance in South Carolina (Bearden, 1961; Lunz, 1965; Olmi, 1986; Wenner and Beatty, in press) and in Texas (Baxter and Renfro, 1967).

Prior studies have shown that *P. aztecus* postlarvae are often more abundant in nighttime collections and on high (flood) tides (Caillouet et al., 1970; Duronslet et al., 1972), similar to the pattern observed in this study. This is probably due to both increased nocturnal activity and decreased gear avoidance at night

[3] Whitaker, J. D. 1982. A possible mechanism for brown shrimp postlarval recruitment. Paper presented at South Carolina Fisheries Workers Assoc. annu. meet., Clemson, SC, 24–25 Feb. 1982. Unpubl. manuscr., 3 p.

Table 2

Mean density (number per 1,000m^3), standard deviation, and number of samples collected for brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*, postlarvae during season of peak ingress at Breach Inlet, South Carolina 1975–92.

	P. aztecus			*P. setiferus*		
Year	Mean	SD	*N*	Mean	SD	*N*
1975	149.9	185.21	98	78.3	265.13	124
1976	119.2	184.83	100	51.7	90.65	104
1977	75.4	105.53	72	0.0	0.00	136
1978	90.1	150.80	40	0.3	1.31	53
1979	86.1	123.80	28	48.5	84.33	25
1980	209.7	144.08	20	2.6	4.17	10
1981	81.1	124.45	26	0.0	0.00	18
1982	—	—	—	9.4	18.16	10
1983	291.2	417.26	13	3.8	6.19	6
1984	125.4	192.53	10	10.5	36.33	39
1985	68.7	101.65	18	2.7	7.35	24
1986	182.7	177.05	14	4.8	19.55	20
1987	58.3	37.38	13	24.7	55.61	14
1988	69.2	112.20	14	10.8	31.55	23
1989	95.2	83.52	20	671.2	1,627.30	25
1990	336.8	348.82	18	29.5	75.82	21
1991	132.1	170.84	18	351.6	452.27	16
1992	129.7	200.25	12	326.6	1,035.87	19

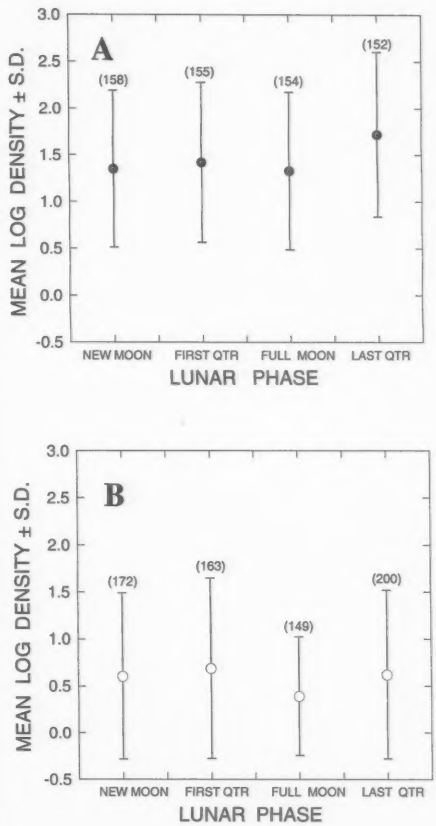


Figure 4

Mean density of postlarval penaeid shrimp (**A**) *Penaeus aztecus* and (**B**) *Penaeus setiferus* grouped by lunar phase during months of peak abundance at Breach Inlet. Samples collected near the bottom on flood tide during daylight (regular sampling). Log Density=log ((number/ 1,000 m^3) + 1). SD=standard deviation. Qtr= quarter. Numbers in parenthesis=number of samples.

(Williams and Deubler, 1968; Matthews et al., 1991). Olmi (1986) in addition to collecting more *P. aztecus* at night, also collected the majority of *P. setiferus* postlarvae at night in a tidal creek in South Carolina. These findings are in agreement with similar studies in the Gulf of Mexico, where *P. setiferus* was found to be more abundant near the surface at night in an inlet (Duronslet et al., 1972) and over a tidal flat (Caillouet et al., 1968). Wenner and Beatty (1993) collected 95% of all penaeid postlarvae at night (including a collection at a creek adjacent to Breach Inlet). In our study, no difference was detected between day and night catches of *P. setiferus*, possibly because we employed a larger net than in the other studies conducted in South Carolina in a higher-velocity tidal flow. This may have minimized avoidance of the gear by postlarvae during daylight. Additional sampling may clarify these observations.

Similar to observations made in our study, Olmi (1986) generally collected fewer postlarvae during full moon phases in South Carolina. Williams and Deubler (1968) in North Carolina and Allen et al. (1980) in the Florida Keys collected fewer *P. duorarum* at night during full moon phases than during new moon phases. Perhaps high light levels at night may delay ingress for several days, causing postlarvae to remain on offshore substrates (Matthews et al., 1991). Peaks in abundance of *P. setiferus* postlarvae may be related to prior spawning activity around new or full moon phases, but this relationship is uncertain at present and warrants further investigation.

A relationship between recruitment of *P. aztecus* postlarvae and subsequent commercial landings has been difficult to demonstrate (Williams, 1969; Ford and St. Amant, 1971; Baxter and Sullivan[4]). Gener-

[4] Baxter, K. N., and L. F. Sullivan. 1986. Forecasting offshore brown shrimp catch from early life history stages. *In* Proc. shrimp yield workshop. Tex. A&M Univ. Sea Grant Rep. TAMU-SG-86-10:22–36.

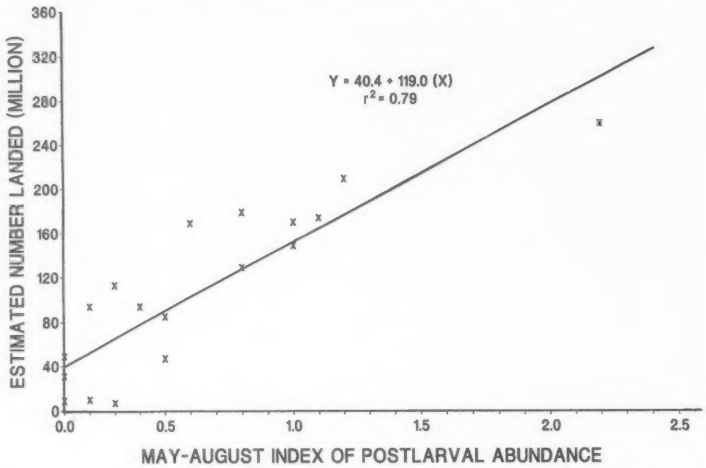


Figure 5

Plot of annual indices of abundance of postlarval white shrimp, *Penaeus setiferus*, versus estimated number of shrimp landed in the fall commercial and recreational fishery, 1975–92.

ally, environmental conditions in the nursery area, e.g. spring temperature and salinity (with related factors such as rainfall, river discharge, and meteorological conditions; Gaidry and White, 1973; Barrett and Gillespie, 1975; Zein-Elden and Renaud, 1986; Childers et al., 1990) are thought to be important influences on production. Biological factors such as predation and secondary production have also been postulated to influence yield (Hunter and Feller, 1987; Gleason and Wellington, 1988; Minello et al., 1989). Postlarval indices have been used with some success in predictive models that incorporate environmental variables and indices of juvenile shrimp abundance (Sutter and Christmas, 1983; Baxter et al., 1988). We have been unsuccessful in efforts to produce a model for brown shrimp production using data from consectutive years, although our postlarval index may be useful in the future.

Undoubtedly many factors influence the production of *P. setiferus* populations, but recent studies have demonstrated that commercial harvest of *P. setiferus* can be modeled (Lam et al., 1989) and apparent spawner-recruit relationships have been described in South Carolina (Lam et al., 1989) and in the Gulf of Mexico (Nance and Nichols, 1988; Gracia, 1991). Our study demonstrates that monitoring of *P. setiferus* postlarvae can be a reliable indicator of harvest.

Expanded sampling effort, i.e. more locations and increased numbers of samples, would perhaps yield more statistically significant results than were obtained at a single location in our study. These data do, however, represent one of the longest-term studies of postlarval penaeid recruitment to date. In addition to contributing to our overall understanding of penaeid shrimp population dynamics, our baseline monitoring effort may be useful as a management tool for predicting harvest and providing advice on optimal times for flooding coastal impoundments for extensive aquaculture.

Acknowledgments

Numerous individuals have contributed to this study, notably C. Bearden, C. Boardman, C. Farmer, L. Leseman, and T. Read. M. Clise assisted with data preparation and K. Swanson prepared the map. E. Wenner and B. Stender reviewed the manuscript.

Literature cited

Aldrich, D. V., C. E. Wood, and K. N. Baxter.
1968. An ecological interpretation of low temperature responses in *Penaeus aztecus* and *P. setiferus* postlarvae. Bull. Mar. Sci. 18:61–71.

Allen, D. M., J. H. Hudson, and T. J. Costello.
1980. Postlarval shrimp (*Penaeus*) in the Florida Keys: species, size and seasonal abundance. Bull. Mar. Sci. 30:21–34.

Anderson, W. W.
1970. Contributions to the life histories of several penaeid shrimps (Penaeidae) along the South At-

lantic coast of the United States. U.S. Fish Wild. Serv. Spec. Sci. Rep. 605, 24 p.

Barrett, B. B., and M. C. Gillespie.
1975. 1975 environmental conditions relative to shrimp production in coastal Louisiana. La. Wild. Fish. Comm. Tech. Bull. 15, 22 p.

Baxter, K. N.
1963. Abundance of postlarval shrimp—one index of future fishing success. Proc. Gulf Caribb. Fish. Inst. 15:79–87.

Baxter, K. N., and W. C. Renfro.
1967. Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. Fish. Bull. 66:149–158.

Baxter, K. N., C. H. Furr Jr., and E. Scott.
1988. The commercial bait shrimp fishery in Galveston Bay, Texas, 1959–87. Mar. Fish. Rev. 50:20–28.

Bearden, C. M.
1961. Notes on postlarvae of commercial shrimp (*Penaeus*) in South Carolina. Contrib. Bears Bluff Lab. 33, 8 p.

Caillouet, C. W., Jr., B. J. Fontenot, Jr., and R. J. Dugas.
1968. Diel fluctuations in catch of postlarval white shrimp, *Penaeus setiferus* (Linnaeus), with Renfro beam trawl. Bull. Mar. Sci. 18:829–835.

Caillouet, C. W., Jr., W. S. Perret, and R. J. Dugas.
1970. Diel fluctuations in catch of postlarval brown shrimp, *Penaeus aztecus* Ives, with the Renfro beam trawl. Bull. Mar. Sci. 20:721–730.

Childers, D. L., J. W. Day, and R. A. Muller.
1990. Relating climatological forcing to coastal water levels in Louisiana estuaries and the potential importance of El Niño-southern oscillation events. Clim. Res. 1:31–42.

Christmas, J. Y., G. Gunter, and P. Musgrave.
1966. Studies of annual abundance of postlarval penaeid shrimp in the estuarine waters of Mississippi, as related to subsequent commercial catches. Gulf Res. Rep. 2:177–212.

Duronslet, M. J., J. M. Lyon, and F. Marullo.
1972. Vertical distribution of postlarval brown, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*, during immigration through a tidal pass. Trans. Am. Fish. Soc. 101:748–752.

Elliot, J. M.
1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Pub. 25, 160 p.

Ford, T. B., and L. St. Amant.
1971. Management guidelines for predicting brown shrimp, *Penaeus aztecus*, production in Louisiana. Proc. Gulf Caribb. Fish. Inst. 23:149–161.

Gaidry, W. J., III, and C. J. White.
1973. Investigations of commercially important penaeid shrimp in Louisiana estuaries. La. Wild. Fish. Comm. Tech. Bull. 8, 154 p.

George, M. J.
1962. Preliminary observations of the recruitment of postlarvae and growth of juveniles of the brown shrimp *Penaeus aztecus* Ives in Barataria Bay. La. Wild. Fish. Comm. Bien. Rep. 9:160–163.

Gleason, D. F., and G. M. Wellington.
1988. Food resources of postlarval brown shrimp (*Penaeus aztecus*) in a Texas salt marsh. Mar. Biol. 97:329–337.

Gracia, A.
1991. Spawning stock-recruitment relationships of white shrimp in the southwestern Gulf of Mexico. Trans. Am. Fish. Soc. 120:519–527.

Hunter, J., and R. J. Feller.
1987. Immunological dietary analysis of two penaeid shrimp species from a South Carolina tidal creek. J. exp. Mar. Biol. Ecol. 107:61–70.

Lam, C. F., J. D. Whitaker, and F. S. Lee.
1989. Model for white shrimp landings for the central coast of South Carolina. North Am. J. Fish. Manage. 9:12–22.

Lindner, M. J., and W. W. Anderson.
1956. Growth, migrations, spawning and size distributions of shrimp, *Penaeus setiferus*. Fish. Bull. 56:553–645.

Loesch, H.
1965. Distribution and growth of penaeid shrimp in Mobile Bay, Alabama. Publ. Inst. Mar. Sci., Univ. Tex. 10:41–58.

Matthews, T. R., W. W. Schroeder, and D. E. Stearns.
1991. Endogenous rhythm, light and salinity effects on postlarval brown shrimp *Penaeus aztecus* Ives recruitment to estuaries. J. exp. Mar. Biol. Ecol. 154:177–189.

Minello, T. J., R. J. Zimmerman, and E. X. Martinez.
1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. Trans. Am. Fish. Soc. 118:693–708.

Nance, J. M., and S. Nichols.
1988. Stock assessments for brown, white and pink shrimp in the U.S. Gulf of Mexico, 1960–1986. NOAA Tech. Memo. SEFC-NMFS-203, 64 p.

Olmi, E. J., III.
1986. Factors affecting the abundance of penaeid shrimps in macroplankton samples from open and impounded brackish marsh systems in South Carolina. M.S. thesis, College of Charleston, Charleston, South Carolina, 95 p.

Pearson, J. C.
1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp, *Penaeus setiferus* (Linn.) Fish. Bull. 49:1–73.

Ringo, R. D., and G. Zamora Jr.
1968. A penaeid postlarval character of taxonomic value. Bull. Mar. Sci. 18:471–476.

Siegel, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, 312 p.

Sutter, F. C., and J. Y. Christmas.
1983. Multilinear models for the prediction of brown

shrimp harvest in Mississippi waters. Gulf Res. Rep. 7:205–210.

Temple, R. F., and C. C. Fischer.

1967. Seasonal distribution and relative abundance of planktonic-stage shrimp (*Penaeus* spp.) in the northwestern Gulf of Mexico, 1961. Fish. Bull. 66:323–334.

Wenner, E. L., and H. R. Beatty.

1993. Utilization of shallow estuarine habitats in South Carolina, USA, by postlarval and juvenile stages of *Penaeus* spp. (Decapoda: Penaeidae). J. Crust. Biol. 13(2):280:295

Williams, A. B.

1959. Spotted and brown shrimp postlarvae (*Penaeus*) in North Carolina. Bull. Mar. Sci. 9:281–290.

1969. A ten-year study of meroplankton in North Carolina estuaries: cycles of occurrence among penaeidean shrimps. Chesapeake Sci. 10:36–47.

Williams, A. B., and E. E. Deubler.

1968. A ten-year study of meroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27–41.

Zein-Elden, Z. P., and M. L. Renaud.

1986. Inshore environmental effects on brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, populations in coastal waters, particularly of Texas. Mar. Fish. Rev. 48 (3):9–19.

Swimbladder deflation in the Atlantic menhaden, *Brevoortia tyrannus*

Richard B. Forward Jr.
Marine Laboratory, School of the Environment, Duke University
Pivers Island, Beaufort, North Carolina 28516-9721

William F. Hettler
Donald E. Hoss
Beaufort Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
Beaufort, North Carolina 28516-9722

Larval clupeoid fishes usually have a pronounced cycle of swimbladder inflation and deflation (Uotani, 1973; Hunter and Sanchez, 1976; Blaxter and Hunter, 1982). Field and laboratory studies of both Atlantic (*Brevoortia tyrannus*; Hoss et al., 1989) and gulf (*Brevoortia patronus*; Hoss and Phonlor, 1984) menhaden found that larvae inflated their swimbladders during the night and deflated them during the day.

Our past studies of Atlantic menhaden larvae found that the cue for inflation is a decrease in light intensity at sunset (Hoss et al., 1989; Forward et al., 1993). Inflation occurs rapidly and begins within 5 minutes of onset of darkness. The process involves moving to the surface, swallowing air into the alimentary canal, and moving this air into the swimbladder through the pneumatic duct (Hoss et al., 1989). Menhaden have no connection (pneumatic duct) between the swimbladder and anus as do some clupeiods (Tracy, 1920). Deflation is less studied. It is hypothesized to occur by diffusion of gas from the swimbladder throughout the night and perhaps by active movement of gas to the alimentary canal and then out through the mouth and anus (Hoss and Phonlor, 1984).

The present study was undertaken to determine 1) the manner in which swimbladder deflation occurs (by diffusion or active gas movement) in Atlantic menhaden larvae, 2) the relationship between deflation and light intensity, 3) the time-course for deflation, and 4) the presence or absence of an endogenous rhythm in deflation.

Materials and methods

Atlantic menhaden, *Brevoortia tyrannus*, were spawned and reared in the laboratory (Hettler, 1983) on a 12:12 hour light-dark cycle with the dark phase beginning at 1900 hours. Lighting during the light phase was provided by daylight fluorescent tubes at a surface intensity of 1.6×10^{15} photons·cm^{-2}·s^{-1} (400–700 nm) as measured with a scalar irradiance meter with a 4π collector (Biospherical Instruments, Inc.). Our previous study found that swimbladder inflation began when larvae were 10 mm total length (TL) but the percentage with inflated swimbladders was low (Forward et al., 1993). Between 11 and 16 mm TL, swimbladders were inflated during the night and deflated during the day. Above 16 mm TL, most fish always had some gas in their swimbladders. Since the percentage of larvae with deflated swimbladders varies between day and night for 11–16 mm TL larvae, they were used in the present experiments.

Deflation was quantified by determining the proportion of larvae with deflated swimbladders. In addition, inflation was quantified by measuring the size of the light-refractive bubbles in the swimbladder and alimentary canal to the nearest 0.02 mm under a microscope. It was assumed that bubbles in the alimentary canal were transported either toward or away from the swimbladder and thereby contributed to the swimbladder volume. Gas bubble volume (v) was calculated by using the equation of Hunter and Sanchez (1976): $V=(4/3)\pi\ ab^2$, where b=half the bubble width and a=half the bubble length. Swimbladder volume was the total volume of all bubbles. Since swimbladder volume increases with larval length (Forward et al., 1993), this relationship is presented when volume is considered. Only larvae with inflated swimbladders were used to calculate the mean volume at each larval length. In contrast, the percentage of larvae with deflated swimbladders was calculated for all larvae (11–16 mm TL), because the previous study found that the proportion of larvae inflating swimbladders did not vary significantly with larval length (Forward et al., 1993).

Four sets of experiments were conducted, all of which began by removing larvae from rearing tanks and by placing them in darkness at the time of the beginning of the dark phase. Our previous study showed that darkness cued initial

Manuscript accepted 22 February 1994.
Fishery Bulletin 92:641–646 (1994).

swimbladder inflation at the beginning of the night (Forward et al., 1993). In all experiments each larva was used only once. It was assumed that all test larvae could potentially inflate their swimbladders in darkness. However, the maximum percent inflation was around 92% (Fig. 1), which suggests that about 8% of the larvae were developmentally incapable of inflation. This low percentage would not alter the overall result of any experiment.

The first experiment measured swimbladder deflation in larvae kept in continuous darkness with and without access to air. Deflation was defined as the absence of gas bubbles in the swimbladder and alimentary canal. Three hours after the beginning of night (2200 hours), a subsample of the larvae was removed from the dark and measured for total length, presence of gas bubbles in the swimbladder and alimentary canal, and for size of the bubbles (standard measurements). There was no evidence that larvae lost or took up gas during the measurement procedure. The remaining larvae were separated into two groups. The first group remained in finger bowls (19.3 cm diameter) in darkness with access to the air-water interface and was similarly sampled during the following day at times (0900, 1200, and 1700 hours) that should have occurred during the normal light phase. The bowls (19.3 cm diameter) containing the second group of larvae were sealed at 2200 hours, so that larvae did not have an air-water interface. The seal was accomplished by filling the bowl completely with water and by placing a Leucite plate over the top so that no air bubbles were present. Larvae were maintained in darkness and were similarly sampled at 0900 and 1700 hours the next day.

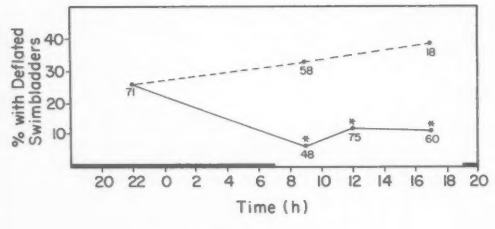


Figure 1

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with no gas in their swimbladder or alimentary canal (deflated) when maintained over time in continuous darkness with (solid line) and without (dashed line) access to the air-water interface. The dark bar indicates the time of the dark phase for the normal light-dark cycle. The number under each point is the sample size. An asterisk indicates the proportion with deflated swimbladders is significantly ($P<0.05$; Z-test for comparison of two proportions) different from that 3 hours after the beginning of the dark phase (initial point).

The second set of experiments was designed to determine the relationship between light intensity and swimbladder deflation. Larvae were placed in darkness at the beginning of the dark phase until two hours (0900) after the time for beginning the light phase. Larvae were then separated into two groups. For the control group standard measurements were made after three more hours of darkness. The second group was irradiated with a constant light intensity for three hours after which standard measurements were made. White light (cool white fluorescent tubes; 1.7×10^{15} photons$\cdot$cm$^{-2}\cdot$s^{-1}) was used in the initial experiment, because this was the normal daytime light during rearing. For determining the change in response with light intensity, the stimulus source was a 300-W incandescent lamp filtered to the blue region with a Corning 4-96 filter. The transmitted wavelengths encompassed the major spectral-sensitivity maxima of most fish (e.g. Munz, 1958; McFarland and Munz, 1975). All intensities below the maximum level were controlled by neutral density filters.

The third set of experiments was designed to determine the time-course for swimbladder deflation. Larvae were maintained as above in darkness until 0900 hours when standard measurements were made on control groups of larvae. The remaining larvae were then exposed to light similar to that used in the normal light phase (cool white fluorescent lamps: intensity=1.7×10^{15} photons$\cdot$cm$^{-2}\cdot$s^{-1}) and standard measurements made on subsamples at various time intervals (5, 15, 30, 60, 90, 120 min).

The fourth experiment tested for the presence of an endogenous rhythm in swimbladder deflation. A large group of larvae was removed from the rearing tank at the beginning of the dark phase and placed in darkness at a constant temperature (22°C) that was similar to the rearing temperature. Standard measurements were then made at time intervals throughout the next 28 hours on subsamples of larvae. Each subsample was placed under blue light (intensity= 4.5×10^{15} photons) for one hour, after which standard measurements were made. Differences in the effect of light on percent deflation over the 28-hour interval would suggest the presence of an endogenous rhythm.

The percentage of larvae with deflated swimbladders and the total volume of bubbles in each larva were calculated for each observation within each experiment. Means, standard deviations, and standard errors of percent data were calculated after the

data were arcsin-transformed. A Z-statistic was used to test differences between two proportions, and a Student's t-test was used to compare mean values of swimbladder volume (Walpole, 1974).

Results

To determine whether deflation was evident at the beginning of the light phase without the onset of light, percent deflation (Fig. 1) and swimbladder volume (Fig. 2) were measured in larvae kept in continuous darkness. When larvae had access to the air-water interface, there was a significant ($P<0.05$; Z-test) decrease in the percentage of fish with deflated swimbladders between three hours after beginning of the dark phase (23%) and two hours after the time for beginning of the light phase (8%). This significant decrease remained throughout the time for the light phase. In contrast, when fish had no access to the air-water interface, the percent deflation did not change significantly (Z-test) over these time intervals (Fig. 1). Thus, larvae do not sequentially inflate their swimbladders at sunset and then deflate them by gas diffusion or active processes by sunrise. Because the percentage of larvae with a deflated swimbladder decreased through the night when larvae had access to the air-water interface, larvae appear to continue to inflate their swimbladders when in darkness. Measurements of swimbladder volume (Fig. 2) support this suggestion.

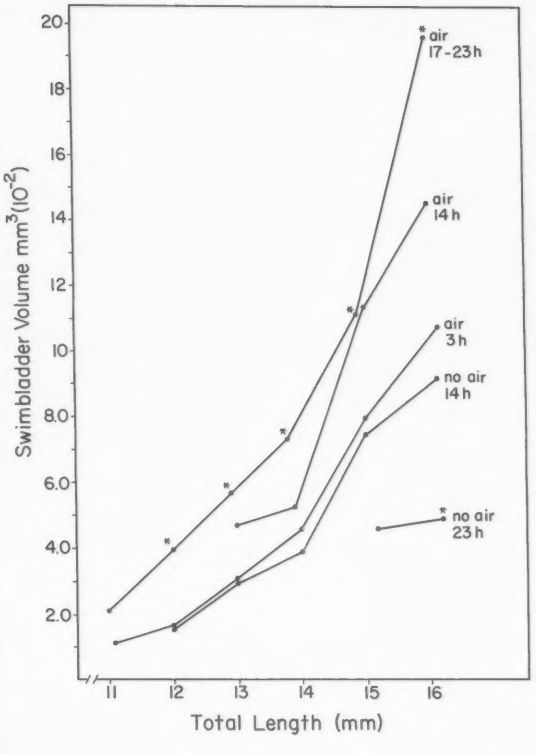


Figure 2

Swimbladder volume for different size larval Atlantic menhaden, *Brevoortia tyrannus*, with (air) and without (no air) access to the air-water interface. The times (e.g. 3 hours) indicate the time in darkness after the beginning of the dark phase when larvae were sampled. Means are plotted and the average sample sizes for calculating the means in each experiment are as follows: air for 17–23 hours=19; air for 14 hours=9; air for 3 hours=19; no air for 14 hours=7; no air for 23 hours=6. The asterisks indicate the mean volume was significantly different ($P<0.05$; Student's t-test) from the mean volume 3 hours after the beginning of the dark phase (air, 3 hours).

The swimbladder volumes over time in darkness with and without access to the air-water interface (Fig. 2) were compared to volumes after inflation at the beginning of the night phase (air, 3 hours) to indicate volume changes due to bubble ingestion and removal, and gas diffusion. Swimbladder volume increased in darkness when fish had access to the air-water interface and decreased when they lacked access. These changes were apparent after 14 hours in darkness but only become statistically significant ($P<0.05$; Student's t-test) after 17–23 hours (Fig. 2).

Thus, larvae with access to the air-water interface continued to actively inflate their swimbladder, whereas swimbladder volume slowly decreased in larvae that lacked this access. Nevertheless, shortly after the beginning of the light phase (Fig. 2; no air, 14 hours), the volumes in larvae without access to air were not significantly lower ($P>0.05$; Student's t-test) than levels after inflation at the beginning of the dark phase (air, 3 hours). Therefore, diffusion of gas from the swimbladder played a very small role in normal deflation at sunrise.

Relation of swimbladder deflation to light

Larvae deflated their swimbladders upon exposure to light. This response was demonstrated in the initial experiment, in which, at the end of the night, larvae were either maintained for three hours in darkness or exposed to white light for this time. The percentage of larvae with a deflated swimbladder in darkness was 12% ($n=75$), whereas the percentage in light was significantly ($P<0.001$; Z-test) greater at 84% ($n=25$). Further studies indicated percent deflation depended upon light inten-

sity (Fig. 3), as the percent deflation increased as light intensity increased. The lowest light intensity to evoke a significant ($P<0.05$; Z-test) increase in deflation (threshold) was 9×10^{12} photons·cm^{-2}·s^{-1}.

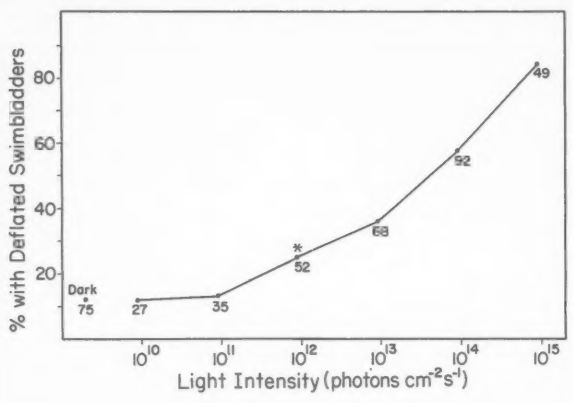


Figure 3

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with deflated swimbladders upon exposure to different light levels and darkness. The number below each point is the sample size. The asterisks indicate the lowest light level at which the proportion deflated was significantly ($P<0.05$; Z-test) greater than the level in darkness.

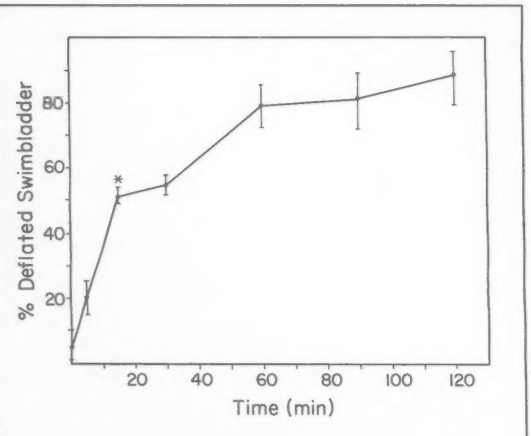


Figure 4

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with deflated swimbladders after different times in light. Means and standard errors are plotted. The average number of replicates was four. The asterisk indicates the first time at which the mean percent was significantly ($P<0.05$; t-test) greater than the initial level (time 0).

Timing of swimbladder deflation

The time course of swimbladder deflation in response to white light was measured upon transfer from darkness to 1.7×10^{15} photons·cm^{-2}·s^{-1}. By producing the maximum rate of light intensity change, it was assumed that the maximum rate of deflation would be evoked. An increase in the percent deflated was evident after 5 minutes and was significantly ($P<0.05$; t-test) greater than the initial level after 15 minutes (Fig. 4). Microscopic examination indicated this rapid deflation was accomplished by passing bubbles from the swimbladder into the gut and then out through both the anus and mouth.

Endogenous rhythm in swimbladder deflation

The percent deflation remained low if larvae were kept in continuous darkness (Fig. 1), which indicates there was no endogenous rhythm in deflation without exposure to light. However, light-cued deflation was not constant over time (Fig. 5). This experiment was conducted twice and involved maintaining larvae in darkness and measuring a subsample after exposure to light for one hour at different times during the solar day. The consistent cycle in both trials was that light-cued deflation was low during the normal dark phase and high during the normal day phase.

An interesting observation was made during these experiments. At the last sampling time, larvae had been in darkness for 27 hours, over which time they continued swimbladder inflation. Exposure to light at 2200 hours caused minimal deflation (Fig. 5). The water containing these larvae also had brine shrimp nauplii from the rearing tank. Larvae are visual predators and had, in effect, been starved for 27 hours in darkness. Under these conditions, once exposed to the light, they began to feed. While measuring swimbladder volumes, their digestive tracts were full of nauplii. Thus, larvae can feed with an inflated swimbladder.

Discussion

Swimbladder deflation by larval Atlantic menhaden is cued by an increase in light intensity. There was no cycle in which larvae inflated their swimbladders at sunset (Forward et al., 1993) and then deflated them gradually over time. In darkness at the end of the night, larvae, with and without air, had inflated swimbladders, and their volumes were not significantly reduced through the night. Thus, deflation

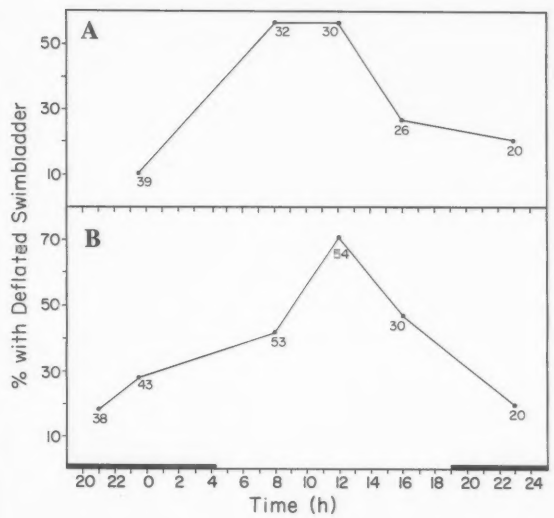


Figure 5

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with deflated swimbladders over the solar day. Larvae were maintained in continuous darkness and then exposed to light for one hour. The experiment was replicated twice (**A** and **B**). The dark bar indicates the time of the normal dark phase of the rearing light-dark cycle. The number under each point is the sample size.

through gas diffusion as suggested by Hoss and Phonlor (1984) did not occur.

If larvae were exposed to light near the time of the beginning of the light phase, deflation began within 5 minutes and was statistically apparent in 15 minutes. Rapid deflation occurred as the pneumatic duct opened between the gut and swimbladder and gas passed into the alimentary canal, where it was moved to both the mouth or anus for expulsion. The lowest light intensity that evoked deflation was about 10^{12} photons·cm^{-2}·s^{-1}. This threshold is below the lowest light intensity that inhibits inflation at sunset (12–16 mm larvae; 6×10^{13} photons·cm^{-2}·s^{-1}; Forward et al., 1993). Thus, larvae appear to be more sensitive to light at sunrise than at sunset. Maximum nighttime light intensity from the moon and star light is about 10^{11} photons·cm^{-2}·s^{-1} (McFarland and Munz, 1975; Lythgoe, 1979). Because this value is below the threshold intensity (10^{12} photons·cm^{-2}·s^{-1}) for deflation, moon and star light probably will not initiate deflation at night. Since surface light levels are about 10^{17} photons·cm^{-2}·s^{-1} at noon (Lythgoe, 1979), an intensity of 10^{12} photons·cm^{-2}·s^{-1} occurs earlier, probably near sunrise.

Larvae appear to have an endogenous rhythm in light-cued deflation. If they were maintained in constant darkness, light induced a low percent deflation during the night phase and a high percentage during the day phase. This rhythm is the reverse of the inflation rhythm, in which sudden darkness initiates inflation at night but rarely during the day (Forward et al., 1993). The functional significance of the deflation rhythm may be that 1) larvae do not deflate their swimbladder at night in response to any light and 2) they are "prepared" for rapid deflation at sunrise.

Field studies suggest Atlantic menhaden larvae undergo nocturnal diel vertical migration (DVM), in which they remain at moderate depths during the day and occur near the surface at night (Govoni and Pietrafesa, in press). Swimbladder inflation at sunset would increase buoyancy and reduce larval sinking rate (Hoss et al., 1989), which would maintain larvae closer to the surface. The present laboratory study supports a nocturnal DVM pattern by indicating that the percentage of larvae with inflated swimbladder and swimbladder volumes increased through the night, when larvae have access to the air-water interface. These increases are not predicted if larvae inflate their swimbladder only once at sunset and then sink. Thus, there is probably a cycle during the night, in which larvae sink while remaining motionless and then periodically return to the surface for additional gas. This pattern would retain larvae near the surface, which may be useful for transport from the offshore spawning area to the mouth of an estuary (Hoss et al., 1989).

A final consideration in the present study is why larvae deflate their swimbladders. Clearly, Atlantic menhaden larvae are adapted for deflation at sunrise. Their rhythm indicates they are most responsive to a light intensity increase at this time, and deflation occurs within 15 minutes. Such a dramatic response suggests deflation has an important functional advantage.

A fully inflated swimbladder may reduce the speed of movement and, thereby, the effectiveness of prey capture. Larvae feed during the day and use vision to find their prey (Blaxter and Hunter, 1982). Although a reduction in capture efficiency is possible, larvae with fully inflated swimbladders can still capture prey as observed in the rhythm experiment. Alternatively, an inflated swimbladder may increase detection of menhaden larvae by visual predators. Since larvae are relatively transparent, the difference in refractive index between air and water increases the contrast between an inflated swim-

bladder and the surrounding water. This increase in visibility could lead to increased predation. Thus, deflation at sunrise may be a predator avoidance response.

Acknowledgments

This research was funded by the National Oceanic and Atmospheric Administration Coastal Ocean Program Office through grant CF92-07 to the North Carolina Sea Grant Program.

Literature cited

Blaxter, J. H. S., and J. R. Hunter.
1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20:1–223.

Forward, R. B., Jr., L. M. McKelvey, W. F. Hettler, and D. E. Hoss.
1993. Swimbladder inflation of the Atlantic menhaden *Brevoortia tyrannus*. Fish. Bull. 91:254–259.

Govoni, J. J., and L. J. Pietrafesa.
In press. Eulerian views of layered water currents, vertical distribution of some larval fishes and inferred advective transport over the continental shelf off North Carolina, USA, in winter. Fish. Oceanography.

Hettler, W. F.
1983. Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. Prog. Fish. Cult. 45:45–48.

Hoss, D. E., and G. Phonlor.
1984. Field and laboratory observations on diurnal swim bladder inflation-deflation in larvae of gulf menhaden, *Brevoortia patronus*. Fish. Bull. 82:513–517.

Hoss, D. E., D. M. Checklery Jr., and L. R. Settle.
1989. Diurnal buoyancy changes in larval Atlantic menhaden (*Brevoortia tyrannus*). Rap. P.-v. Reun. Cons. int. Explor. Mer. 191:105–111.

Hunter, J. R., and C. Sanchez.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull. 74:847–855.

Lythgoe, J. N.
1979. The ecology of vision. Clarendon Press, Oxford, 244 p.

McFarland, W. N., and F. W. Munz.
1975. The evolution of photopic visual pigments in fish. Vision Res. 15:1071–1080.

Munz, F. W.
1958. The photosensitive retinal pigments of fish from relatively turbid coastal waters. J. Gen. Physiol. 42:445–459.

Tracy, H. C.
1920. The membranous labyrinth and its relation to the precoelomic diverticulum of the swimbladder in clupeoids. J. Comp. Neurol. 31:219–257.

Uotani, L.
1973. Diurnal changes of gas bladder and behavior of postlarval anchovy and other related species. Bull. Jpn. Soc. Sci. Fish. 39:867–876.

Walpole, R. E.
1974. Introduction to statistics. Macmillan, New York.

An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977–1986

Sharon L. Gilman

University of Rhode Island, Narragansett Bay Campus
Narragansett, Rhode Island 02882

The northern sand lance, *Ammodytes dubius*, is a small planktivorous fish, classified as a "ubiquitous shelf species" (Sherman et al., 1983) and is found off the northwest Atlantic coast from North Carolina to Greenland (Nizinski et al., 1990). Sand lance are consumed by many piscivorous marine vertebrates. They have been found in the stomachs of dogfish, *Squalus* spp., skates, *Raja* spp., Atlantic cod, *Gadus morhua*, haddock, *Melanogrammus aeglefinus*, pollock, *Pollachius virens*, sculpin, *Myoxocephalus* spp., Atlantic salmon, *Salmo salar*, various flatfishes, *Paralichthys*, *Limanda*, and *Pseudopleuronectes*, and other fishes (Scott, 1968; Reay, 1970; Meyer et al., 1979; Bowman and Michaels, 1981; Winters, 1981), as well as seabirds (Backus and Bourne, 1987). Humpback whales, *Megaptera novaeangliae*, have also been observed feeding on sand lance (Payne et al., 1986). Negative correlations have been shown between the abundance of sand lance and right whales, *Eubalaena glacialis*, and it has been suggested that in the northwest Atlantic these two animals may actually compete for their primary food source, the copepod *Calanus finmarchicus* (Kenney et al., 1986; Payne et al., 1990). Therefore, although the sand lance is not commercially important, as a plankton feeder and an important prey species, it may exert significant influence over the efficiency of energy transfer from primary to higher trophic levels.

Georges Bank was chosen as a study area in which dramatic changes in the northern sand lance population might be examined in terms of the consumption and production of fish relative to the production of the region as a whole. This 41,809 km^2, 50-m deep plateau (Sherman et al., 1984) is located off the northeast coast of the United States and is a highly productive fishing ground with high annual primary production (350 g carbon$\cdot m^{-2} \cdot y^{-1}$) owing to the retention of nutrients (Sherman et al., 1984; Backus and Bourne, 1987). Because of its commercial significance, Georges Bank has been well studied. Energy budgets have been developed for the entire Bank (Cohen et al., 1982; Jones, 1984; Sissenwine et al., 1984) and offer a convenient way to examine the significance of the consumption and production of an individual species within an important area of the Northeast Shelf ecosystem.

Individual energy budgets of fish have been developed for many species (Edwards et al., 1972; Adams, 1976; Kitchell et al., 1977; Kitchell and Breck, 1980; Cho et al., 1982; Kerr, 1982; Diana, 1983; Durbin and Durbin, 1983; Rice and Cochran, 1984; Kerr and Dickie, 1985; Cui and Wooton, 1989). In this study, the energy budget of the northern sand lance was developed from experiments that measured the following parameters: growth, metabolism, feeding and assimilation efficiency (Larimer, 1992), and reproductive production. These parameters were assembled into an annual energy budget based on the daily activity of the fish in the field associated with temperature and food availability. Monthly growth was used to estimate annual ration and the budget was extrapolated to northern sand lance population abundance levels measured on Georges Bank from 1977 to 1986.[1] The potential predatory impact of the northern sand lance population on seasonal and annual zooplankton productivity on the bank[2] (Sherman et al., 1987) was examined. Finally, the annual production and consumption by these populations were compared with energy budget model values for Georges Bank.

Methods

Individual energy budget

An "average" adult northern sand lance was considered to be age 1+, the dominant age in a population of adults (Nelson, 1990). The average size was 142 mm fork length, 6.02 g wet weight, and 1.40 g dry weight based on the following wet-weight fork length relationship of Larimer (1992):

$$\text{weight} = 4.0665\ e^{-4}\ \text{length}^{3.61}.$$

The annual energy budget for an individual northern sand lance was described by the following equation adapted from Winberg (1956):

[1] Kane, J. 1992. Macrozooplankton seasonal abundances on Georges Bank, 1977–1986. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Narragansett Lab., Narragansett, RI 02882. Unpubl. data.

[2] Fogarty, M. 1992. Survey biomass estimates for sand lance on Georges Bank. NOAA, Nat. Mar. Fish. Ser., Northeast Fish Sci. Center, Water Street, Wood's Hole, MA 02543. Unpubl. data.

Manuscript accepted 16 February 1994.
Fishery Bulletin 92:647–654 (1994).

$$G + R = C - M - W, \quad (1)$$

where the components (in kilocalories) are

G = somatic growth;
R = reproduction;
C = food consumption;
M = metabolism;
W = fecal loss.

Assimilated ration (A) equals consumption minus fecal losses. A small fraction of the assimilated energy is lost through nitrogenous excretion (Brett and Groves, 1979) but was not estimated in this study. The remaining portion of the assimilated energy was assumed available for growth and metabolism. The methods used to estimate each parameter are described below.

Growth

The northern sand lance growth rate is 0.87 yr^{-1} in grams, as determined by back calculation of length at age from otolith increments (Larimer, 1992). Multiplied by 6.02 g, the wet weight of an average fish, this is equivalent to a growth rate of 5.24 $g \cdot yr^{-1}$. Wet weight was converted to dry weight using the following equation (Larimer, 1992):

$$\text{dry wt.} = 0.309 \text{ wet wt.} - 0.286 \ (r^2 = 0.859).$$

The growth rate (in dry grams) was 1.20 $g \cdot fish^{-1} \cdot yr^{-1}$. Growth in kilocalories was calculated based on a mean caloric content of 6.73 $kcal \cdot dry\ gram^{-1}$ (Larimer, 1992) and was 8.08 $kcal \cdot fish^{-1} \cdot yr^{-1}$.

Growth was also estimated on a monthly basis. Reay (1972) measured monthly growth in length of age 1+ *A. tobianus* off the coast of England. These fish and *A. dubius* are of similar size (range: 84–138 mm, Reay, 1972, versus 85–138 mm, Larimer, 1992) and seasonal temperatures in their habitats are similar (3–19°C off England, Reay, 1972; 3.4–14.4°C for Georges Bank, Hopkins and Garfield, 1981). Therefore, I assumed that their monthly growth rates would be similar. Reay (1972) found that *A. tobianus* grows from April to October; however, it spawns from February to March, later than the December to February spawning of *A. dubius* (Bigelow and Schroeder, 1953; Norcross et al., 1961; Reay, 1970; Colton et al., 1979; Sherman et al., 1984). Nelson and Ross (1991) found that gonadal development of *A. dubius* on Georges Bank was in progress by September. Thus, I assumed that *A. dubius* weight gain beginning in September is devoted to gonadal rather than to somatic growth, and therefore, their somatic growing season extends from April to August.

The percentage of annual growth occurring during each month of the growing season was calculated from two years of monthly growth data for *A. tobianus* as reported by Reay (1972). This monthly average was multiplied by the total annual growth measured for *A. dubius* (8.08 $kcal \cdot yr^{-1}$, see above) to determine monthly net growth in caloric content.

Reproductive energetics

Gonad weight and caloric content were measured to estimate the portion of the northern sand lance annual energy budget devoted to reproduction. In December 1990, eight fish judged to be ripe (stage III, of Macer, 1966) were measured (fork length, mm), and wet weighed (g). The gonads were extracted, weighed and dried. The dried gonads were weighed, ground to a powder with mortar and pestle, and their caloric content measured with a Phillipson microbomb calorimeter (Phillipson, 1964).

Metabolism

Metabolism was estimated for an "average" day in each month by using mean monthly water temperature calculated from averages of the top 40 m on Georges Bank (Hopkins and Garfield, 1981) and the number of hours of daylight at mid-month. I assumed the fish actively feed during half of the daylight hours. Thus, I divided a day into three periods: a nighttime resting period equivalent to the hours of darkness, a feeding period that is assumed to be half of the daylight hours, and a postfeeding period that is the remaining half of the daylight hours. Metabolic rates were estimated for each of these periods from the rates measured during similar periods at 6, 12, and 18°C (Larimer, 1992). The lowest temperature that could be maintained in the lab was 6°C so these temperatures were chosen as the best approximation of the annual temperature range on Georges Bank (Backus and Bourne, 1987). Because there was no clear relationship between metabolic rates and temperature evident in the respiration experiments (Larimer, 1992), the 6°C values were used for April, May, and December, the 12°C values were used for June, July, October, and November, and the 18°C values were used for August and September.

Assimilation efficiency

The efficiency of energy assimilation by sand lance was determined by the monthly temperature on Georges Bank (Backus and Bourne, 1987) and the relationship of assimilation efficiency to temperature found in Larimer (1992):

$$AE = 82.41 + 0.764\ T, \quad (2)$$

where AE = assimilation efficiency (%);
T = temperature (°C).

Ration estimation

Annual ration was estimated by summing the metabolic requirements, somatic growth requirements, and reproductive requirements, and then by taking assimilation efficiency into account. Because assimilation efficiency was found to increase with increasing temperature (Larimer, 1992), ration was calculated on a monthly rather than an annual basis.

Seasonal water temperatures (and therefore fish activity levels) and food availability on Georges Bank were used to estimate a monthly ration for sand lance based on the energy budget requirements. I assumed that the fish are inactive during January, February, and March. Other species of *Ammodytes* (*A. tobianus*, Reay, 1970; *A. marinus*, Macer, 1966) are known to spend the winter months buried in the sand. This behavior has not been recorded for *A. dubius* but catches of these fish during the winter months are low (Nelson, 1990) and they have been observed to spend extended periods buried in the sand in the laboratory, apparently without feeding[3] (personal observ., 1991). I assumed that the metabolic requirement for January, February, and March and the annual reproductive requirement were assimilated from May through September when food availability is high and water temperatures are still warm.

Monthly gross energy requirements were estimated by summing monthly energetic costs and multiplying by the percent of consumed calories lost as waste based on monthly assimilation efficiencies. These were divided by the caloric content of the ration (6.11 ± 0.77 kcal·g^{-1} for *Calanus finmarchicus*; Larimer, 1992) to determine the actual grams of ration required per month. The sum of these monthly estimates is the yearly ration requirement.

Population energy budget

The energy budget for individual adult northern sand lance was extrapolated to the population level by multiplying overall production (growth+reproduction) and consumption (predicted ration) by the number of individuals estimated to be present on Georges Bank from 1977 through 1986. Northern sand lance population size was estimated from spring sand lance biomass estimates for 1977–86.[2] Mean sand lance weight per tow was divided by mean individual adult fish wet weight (see above) and the average tow volume to estimate the number of individuals present per unit volume on the Bank. There were no sand lance abundance data for 1979. The energy budget parameters of the population were then compared with estimates of secondary production on Georges Bank.

Macrozooplankton production (including *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages* species, and *Metridia lucens*) on Georges Bank was calculated from population estimates measured during the MARMAP surveys from 1977 to 1986 (Sherman et al., 1987). Zooplankton volumes were reported in Kane.[1] These were transformed into annual production values following Sherman et al. (1987) where volume is converted to biomass using the following equation (Wiebe et al., 1975):

$$\log_{10}(\text{dry weight}) = \log_{10}(\text{volume} + 1.828)/0.848.$$

A value of 5.25 kcal·g^{-1} (Laurence, 1976) and a production-to-biomass ratio (P:B) of 7 (Steele, 1974; Crisp, 1975) were used to convert zooplankton biomass to production. Annual production was estimated for each year of available zooplankton data (1977–86) and compared with the calculated annual consumption by northern sand lance.

Results and discussion

Predicted ration and individual budget

The ratio of production to consumption (P:C) determined from an individual energy budget represents the gross ecological growth efficiency of an animal within a trophic level (Slobodkin, 1960). This ratio was determined from the individual energy budget for the northern sand lance. Monthly growth estimates calculated from Reay's (1972) data range from 0% from September to March to 36% dry body weight in May (Table 1) and from 0.00 kcal, from Septem-

Table 1

Monthly somatic growth of northern sand lance, *Ammodytes dubius*, on Georges Bank estimated from measurements of *A. tobianus* growth rates in length (Reay, 1972) and the availability of food on the Bank. Reay measured no net growth September through March.

Month	% Growth (wt)	Growth (kcal)
April	0.14	1.15
May	0.36	2.90
June	0.19	1.50
July	0.07	0.56
August	0.24	1.97

[3] Halavik, T. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Narragansett Lab, Narragansett, R.I. 02882. Personal commun., September 1991.

Table 2

Monthly energy requirements for northern sand lance, *Ammodytes dubius*, on Georges Bank. Fish are assumed to be inactive in January, February, and March; therefore metabolic energy requirements for those months ("nonfeed metabolism"), as well as annual reproductive energy requirements, were divided equally over the months of highest temperature and food availability.

Month	Metabolic cost (kcal)	Somatic growth (kcal)	Reproductive growth (kcal)	Nonfeed metabolism (kcal)	Energy required (kcal)
January	2.23	0.00	0.00	0.00	0.00
February	2.02	0.00	0.00	0.00	0.00
March	2.23	0.00	0.00	0.00	0.00
April	3.90	1.15	0.00	0.00	5.05
May	4.15	2.90	0.49	1.29	8.83
June	3.33	1.50	0.49	1.30	6.62
July	3.38	0.56	0.49	1.30	5.73
August	3.57	1.97	0.49	1.30	7.33
September	3.33	0.00	0.49	1.29	5.11
October	3.07	0.00	0.00	0.00	3.07
November	2.91	0.00	0.00	0.00	2.91
December	3.44	0.00	0.00	0.00	3.44

Table 3

Gonad weight and energy content of northern sand lance, *Ammodytes dubius*, from Georges Bank.

	Males	Females	Total mean
N	1	7	8
Fork length (mm)	132	127±7.4	128±7.1
Dry weight (g)	1.23	1.22±0.35	1.23±4.94
Gonad (% dry body weight)	14.33	26.36±2.72	24.85±4.94
Gonad (kcal/g)	6.4	7.12±0.52	7.03±0.54

Table 4

Calculated monthly respiration requirements in kilocalories for northern sand lance, *Ammodytes dubius*, on Georges Bank. Fish are assumed to be inactive from January to March.

Month	°C	Hours of light	Kcal used per month
January	6.1	9.5	2.23
February	4.3	10.5	2.02
March	3.4	12.0	2.23
April	3.4	13.5	3.90
May	7.7	14.5	4.15
June	10.9	15.5	3.33
July	13.0	15.0	3.38
August	14.4	14.0	3.57
September	14.3	12.5	3.33
October	13.2	11.0	3.07
November	11.0	10.0	2.91
December	8.8	9.0	3.44
Annual total			37.56

ber to March, to 2.90 kcal in May (Table 2). The mean percent of body weight accounted for by the ripe gonads, 24.85%, is similar to the 20–30% measured for age 1+ *A. personatus* (Okamoto et al., 1989) and the 25–28% measured for both male and female *A. americanus* (Smigielski et al., 1984), (Table 3). Estimated monthly metabolic requirements range from a low in February of 2.03 kcal to a high in May of 4.15 kcal (Table 4). The annual individual energy requirement was 37.56 kcal (Table 4). Monthly assimilation efficiencies and daily rations are shown in Table 5, and the predicted annual ration is 52.62 kcal·fish^{-1} or 8.60 g·fish^{-1} (assuming a caloric content of 6.11 kcal·g^{-1} for *C. finmarchicus*; Larimer, 1992). The energy assimilated from that ingested is 48.09 kcal·fish^{-1} so the annual individual energy budget in terms of kilocalories is approximated by

$$(G) + (R) = (AR) - (R), \quad (3)$$

where growth (G) = 8.08 kcal·yr^{-1};
reproduction (R) = 2.45 kcal·yr^{-1};
assimilated ration (AR) = 48.09 kcal·yr^{-1};
respiration (R) = 37.56 kcal·yr^{-1}.

If the budget is converted into percentage of total consumption accounted for by each parameter, the following relationship results:

Table 5

Predicted daily ration of adult northern sand lance, *Ammodytes dubius*, on Georges Bank based on monthly growth (Table 1) and assimilation efficiency for *Calanus finmarchicus* (Equation 2).

Month	Assimilation efficiency (%)	Required energy (kcal/month)	Ration (kcal/month)	Ration (g/month)	Daily ration (% body wt)
January	87.07	0.00	0.00	0.00	0.00
February	85.70	0.00	0.00	0.00	0.00
March	85.01	0.00	0.00	0.00	0.00
April	85.01	5.05	5.81	0.95	2.26
May	88.29	8.83	9.86	1.61	3.72
June	90.74	6.62	7.23	1.18	2.82
July	92.34	5.73	6.17	1.01	2.33
August	93.41	7.33	7.81	1.28	2.95
September	93.34	5.11	5.45	0.89	2.12
October	92.49	3.07	3.30	0.54	1.24
November	90.81	2.91	3.18	0.52	1.24
December	89.13	3.44	3.81	0.62	1.44
Annually		48.09	52.62	8.60	

Table 6

Annual consumption of adult northern sand lance, *Ammodytes dubius*, on Georges Bank, based on individual energy budget requirements extrapolated to population levels from 1977 through 1986. These values are compared to average annual zooplankton productivity for each year. The percent of production consumed by sand lance is shown for each year.

Year	Sand land abundance (no. per m^3)	Annual consumption ($kcal/m^3/yr$)	Zooplankton production ($kcal/m^3/yr$)	% consumed by sand lance
1977	0.0198	1.03	45.56	2.27
1978	0.0261	1.63	32.07	5.08
1980	0.0782	4.07	21.16	19.24
1981	0.0143	0.74	22.89	3.24
1982	0.0261	1.36	16.25	8.37
1983	0.0091	0.48	12.77	3.76
1984	0.0056	0.29	14.56	1.99
1985	0.0032	0.17	21.58	0.79
1986	0.0081	0.42	18.49	2.27

$$100C = 15G + 5R + 71M + 9W, \quad (4)$$

where C = consumption;
G = growth;
R = reproduction;
M = metabolic requirement;
W = waste (that portion of the predicted ration that is not assimilated based on Equation 2 above).

For an individual adult northern sand lance on Georges Bank, total production is 10.53 $kcal \cdot yr^{-1}$ (growth+reproduction), and total consumption is 52.62 $kcal \cdot yr^{-1}$(Table 5); therefore, ecological efficiency is 20.0%.

Population energy budget

Northern sand lance consumed a significant proportion of total annual zooplankton production of Georges Bank from 1977 through 1986. Population abundance of northern sand lance from 1977 through 1986 was negatively correlated with zooplankton abundances during the same period (r^2=0.683, P<0.05; Fig. 1). Northern sand lance consumed 0.79–19.24% of the annual zooplankton production from 1977 to 1986 (Table 6; Fig. 2).

The trophic efficiency of the northern sand lance is 20%, according to the present energy budget model. Jones's (1984) Georges Bank energy model found that

the primary productivity of the Bank adequately accounted for fish production only if a trophic transfer efficiency of greater than 10% was assumed. This may be a valid assumption for the model at the trophic level of the northern sand lance.

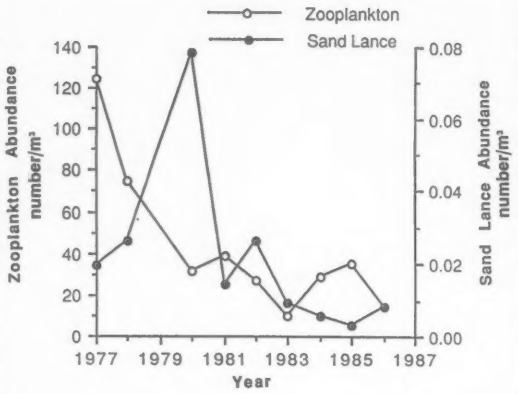


Figure 1

Average annual copepod abundance of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages hamatus*, *C. typicus*, *Metridia lucens*, and of adult northern sand lance, *Ammodytes dubius*, on Georges Bank from 1977 through 1986.

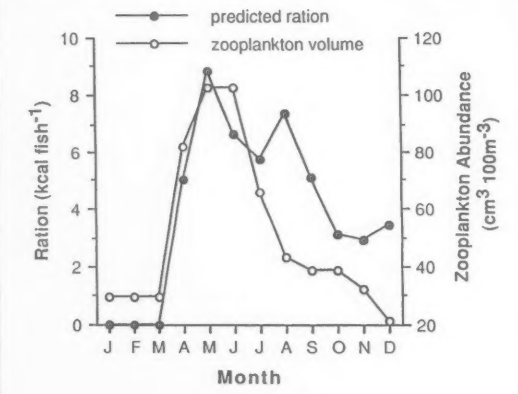


Figure 2

Mean monthly zooplankton biomass of *Calanus finmarchicus*, *Pseudocalanus* species, *Paracalanus parvus*, and *Centropages* species on Georges Bank (Sherman et al., 1987) and monthly ration required for an individual adult northern sand lance, *Ammodytes dubius*, based on the individual energy budget.

In their budget of Georges Bank bioenergetics, Sissenwine et al. (1984) place sand lance in their "other finfish" compartment (all nonfished species that are vulnerable to fishing gear). From 1973 to 1975 a consumption of 9.3 $kcal \cdot m^{-2} \cdot y^{-1}$ was attributed to this category. Sissenwine et al. (1984) suggested that the impact of the sand lance population was underestimated in their budget, and it appears from the present study, based on the individual energy budget and population size, that this error was potentially significant. By converting population energetic consumption on Georges Bank (Table 6) to consumption per square meter (assuming a mean depth on the Bank of 50 m; Backus and Bourne, 1987), sand lance consumed from 8.5 to 203.5 $kcal \cdot m^{-2} \cdot y^{-1}$ from 1977 to 1986. This represents nearly all the consumption attributed to the "other finfish" at low northern sand lance abundances and over 20 times the total "other finfish" consumption at high northern sand lance abundances. The results of this study suggest that the budget estimates of annual consumption by exploitable but commercially undesirable fishes may need to be revised upward.

Acknowledgments

Special thanks to Ken Sherman, director of the Narragansett Lab of the National Marine Fisheries Service, for his enthusiasm and assistance in introducing me to his associates, Jack Green and Mike Fogarty, who provided me with the most up to date population data for zooplankton and sand lance on Georges Bank. The Ph.D. dissertation in which this study is detailed is cataloged at the Univ. Rhode Island under the name S. Larimer.

Literature cited

Adams, S. M.
1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. II: Functional analysis. J. exp. Mar. Biol. Ecol. 22:293–311.

Backus, R. H., and D. W. Bourne (eds.).
1987. Georges Bank. M.I.T. Press, Cambridge, MA, 593 p.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. Fish. Bull. Fish and Wildl. Ser. 53, 577 p.

Bowman, R. E., and W. Michaels.
1981. Food habits of seventeen species of northwest Atlantic fish. NOAA Tech. Memo. NMFS-F/NEC-28.

Brett, J. R., and T. D. D. Groves.
1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish physiology, Vol. 8. Academic Press, 786 p.

Cho, C. Y., S. J. Slinger, and H. S. Bayley.
1982. Bioenergetics of salmonid fishes: energy, intake, expenditure, and productivity. Comp. Biochem. Physiol. 73B:25–41.

Cohen, E. B., M. D. Grosslein, M. P. Sissenwine, F. Steimle, and W. R. Wright.
1982. An energy budget for Georges Bank. Can. Spec. Publ. Fish. Aquat. Sci. 59:95–107.

Crisp, D. J.
1975. Secondary productivity in the sea. *In* D. F. Reichle, J. F. Franklin, and D. W. Goodal (eds.), Productivity of world ecosystems, p. 71–90. Washington, D.C., National Academy of Sciences.

Cui, Y., and R. J. Wooton.
1989. Bioenergetics of growth of a cyprinid *Phoxinus phoxinus* (L.): development and testing of a growth model. J. Fish Biol. 34:47–64.

Diana, J. S.
1983. An energy budget for northern pike (*Esox lucius*). Can. J. Zool. 61:1968–1975.

Durbin, E. G., and A. G. Durbin.
1983. Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae), a filter feeding planktivore. Fish. Bull. 81:177–199.

Edwards, R. R. C., D. M. Finlayson, and J. H. Steele.
1972. An experimental study of oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). J. exp. Mar. Biol. Ecol. 8:299–309.

Hopkins, T. S., and N. Garfield III.
1981. Physical origins of Georges Bank water. J. Mar. Res. 39:465–500.

Jones, R.
1984. Some observations on energy transfer through the North Sea and Georges Bank food webs. Rapp. P.-v. Reun. Cons. int. Explor. Mer 183:204–217.

Kenney, R. D., M. A. M. Hyman, R. E. Owen, G. P. Scott, and H. E. Winn.
1986. Estimation of prey densities required by western North Atlantic right whales. Mar. Mammal Sci. 2:1–13.

Kerr, S. R.
1982. Estimating the energy budgets of actively predatory fishes. Can. J. Fish. Aquat. Sci. 39:371–379.

Kerr, S. R., and L. M. Dickie.
1985. Bioenergetics of 0+ Atlantic herring (*Clupea harengus harengus*). Can. J. Fish. Aquat. Sci. 42:105–110.

Kitchell, J. F., and J. E. Breck.
1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37:2159–2168.

Kitchell, J. F., D. J. Stewart, and D. Weininger.
1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1922–1935.

Larimer, S.
1992. Aspects of the bioenergetics and ecology of sand lance of Georges Bank. Ph.D. diss., Univ. Rhode Island, 300 p.

Laurence, G. C.
1976. Caloric values of some north Atlantic calanoid copepods. Fish. Bull. 741:218–220.

Macer, C. T.
1966. Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. Fish. Invest. Lond. Ser. 2, 24:1–55.

Meyer, T. L., R. A. Cooper, and R. W. Langton.
1979. Relative abundance and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. Fish. Bull. 77:243–253.

Nelson, G. A.
1990. Population biology and dynamics of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight region. M.S. thesis, Univ. Mass., 202 p.

Nelson, G. A., and M. R. Ross.
1991. Biology and population changes of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight. J. Northwest Atl. Fish. Sci. 11:11–27.

Nizinski, M. S., B. B. Collette, and B. B. Washington.
1990. Separation of two species of sand lances, *Ammodytes americanus* and *A. dubius*, in the western North Atlantic. Fish. Bull. 88:241–255.

Norcross, J. J., W. H. Massmann, and E. B. Joseph.
1961. Investigations on Investigations on inner continental shelf waters off lower Chesapeake Bay. Part II: Sand lance larvae, *Ammodytes americanus*. Chesapeake Sci. 2:49–59.

Okamoto, H., H. Sato, and K. Shimazi.
1989. Comparison of reproductive cycle between two genetically distinctive groups of sand lance (genus *Ammodytes*) from northern Hokkaido. Nippon Suisan Gakkaishi 55:1935–1940.

Payne, P. M., J. R. Nicolas, L. O'Brien, and K. D. Powers.
1986. The distribution of the humpback whale *Megaptera novaeangliae* on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel *Ammodytes americanus*. Fish. Bull. 84:271–277.

Payne, P. M., D. N. Wiley, S. B. Young, S. Pittman, P. J. Clapham, and J. W. Jossi.
1990. Recent fluctuations in the abundance of baleen whales in the southern Gulf of Maine in relation to changes in selected prey. Fish. Bull. 88:687–696.

Phillipson, J.
1964. A miniature bomb calorimeter for small biological samples. Oikos 15:130–139.

Reay, P. J.
1970. Synopsis of biological data on North Atlantic sand eels of the genus *Ammodytes*. F.A.O. Fisheries Synopsis 82, 71 p.
1972. The seasonal pattern of otolith growth and its application to back-calculation studies in

Ammodytes tobianus L. J. Cons. int. Explor. Mer 34:485–504.

Rice, J. A., and P. A. Cochran.
1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65:732–739.

Scott, J. S.
1968. Morphometrics, distribution, growth, and maturity of offshore sand lance (*Ammodytes dubius*) on the Nova Scotia banks. J. Fish. Res. Board Can. 25:1775–1785.

Sherman, K., R. Lasker, W. Richards, and A. W. Kendall Jr.
1983. Ichthyoplankton and fish recruitment studies in large marine ecosystems. Mar. Fish. Rev. 45:1–25.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont.
1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Serv. 18:1–19.

Sherman, K., W. G. Smith, J. R. Green, E. B. Cohen, M. S. Berman, K. A. Marti, and J. R. Goulet.
1987. Zooplankton production and the fisheries of the northeastern shelf. *In* R. H. Backus and D. W. Bourne (eds.), Georges Bank, p. 268–282. M.I.T. Press, Cambridge, MA.

Sissenwine, M. P., E. B. Cohen, and M. D. Grosslein.
1984. Structure of the Georges Bank ecosystem. Rapp. P.-v. Reun. Cons. int. Explor. Mer 183:243–254.

Slobodkin, L. B.
1960. Ecological energy relationships at the population level. Am. Nat. 94:213–236.

Smigielski, A. S., T. A. Halavik, L. J. Buckley, S. M. Drew, and G. C. Laurence.
1984. Spawning, embryo development, and growth of the American sand lance *Ammodytes americanus* in the laboratory. Mar. Ecol. Prog. Ser. 14:287–292.

Steele, J. H.
1974. The structures of marine ecosystems. Harvard Univ. Press, Cambridge, MA, 128 p.

Wiebe, P. H., S. Boyd, and J. L. Cox.
1975. Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. Fish. Bull. 73:777–786.

Winberg, G. G.
1956. Rate of metabolism and food requirements of fishes. Belorussian State Univ., Minsk. Fish. Res. Board Can. Transl. Ser. 194, p. 1–256.

Winters, G. H.
1981. Growth patterns in sand lance, *Ammodytes dubius*, from the Grand Bank. Can. J. Fish. Aquat. Sci. 38:841–846.

Movements of tagged adult yellowtail rockfish, *Sebastes flavidus*, off the west coast of North America

Richard D. Stanley
Bruce M. Leaman
Pacific Biological Station
Department of Fisheries and Oceans, Canada
Nanaimo, British Columbia, V9R 5K6

Lewis Haldorson
Juneau Center, School of Fisheries and Ocean Sciences,
University of Alaska, Fairbanks
11120 Glacier Highway
Juneau, Alaska 99801-8677

Victoria M. O'Connell
Alaska Department of Fish and Game
304 Lake Street, Room 103,
Sitka, Alaska 99835

The Department of Fisheries and Oceans, Canada, and the University of Alaska conducted independent tagging studies on yellowtail rockfish, *Sebastes flavidus*, in the early 1980's. The Canadian study was designed to validate ageing methodology for rockfishes (Leaman and Nagtegaal, 1987). The Alaskan study was part of a larger survey of nearshore bottomfish resources in southeastern Alaska.[1,2] While neither study was designed to quantify the extent of this species' movement, the recoveries provided new insight into rockfish behavior and new implications for the management of this species.

Tagging studies of shallow demersal (<100 m) species of rockfish, *Sebastes* spp., have typically indicated very limited movement (Table 1), with the exception of a report of a brown rockfish, *S. auriculatus*, that travelled over 50 km from San Francisco Bay.[3] Authors have also suggested limited movement for the deeper demersal or "slope" rockfish species, such as Pacific ocean perch, *S. alutus*, that are found along the continental slope at depths greater than 200 m (Fadeev, 1968; Gunderson, 1971; Wishard et al., 1980; Leaman and Kabata, 1987). While they appear to make seasonal bathymetric migrations, the available evidence from commercial fishing patterns, parasite occurrence, and age/size compositions have led investigators to hypothesize that these species make very limited latitudinal movements along the continental shelf. However, because of decompression and other injuries associated with surfacing from depths of over 200 m, no tagging studies have been performed to test this hypothesis.

It is the semi-pelagic species that inhabit the continental shelf (100–200 m) which appear to exhibit significant movement. Studies of black rockfish, *S. melanops*, and immature yellowtail rockfish indicate that at least some individuals move long distances. In northern Puget Sound (Fig. 1), Mathews and Barker (1983) tagged 123 black and 153 yellowtail rockfish. Three of eight black rockfish and eight of 10 confirmed yellowtail rockfish recoveries came from the west coast of Washington at distances up to 400 km from the release site. Because the yellowtail rockfish were all immature, the authors proposed an ontogenetic movement offshore in conjunction with reproductive maturation. Similarly, Barss[4] reported that 12 of 23 recovered immature canary rockfish, *S. pinniger*, travelled more than 100 km along the Oregon coast. Culver (1987) provided the first evidence of long distance movement of adult or reproductively mature rockfish. He recovered 484 tags from 14,795 black rockfish tagged off Washington and northern Oregon. One fish, which had been tagged off Oregon, was recovered off northern California, 555 km south of its release site. More than 12% of the recovered black rockfish moved farther than 80 km.

Contrary to those reports, which documented long distance move-

[1] Rosenthal, R. J., L. J. Field, and D. Meyer. 1981. Survey of nearshore bottomfish in the outside waters of southeastern Alaska. Alaska Coastal Research, P. O. Box 368, Langley WA, 98260. Final report to State of Alaska, Dep. Fish Game, Comm. Fish. Div. Juneau, 84 p.

[2] Rosenthal, R. J., L. Haldorson, L. J. Field, and V. M. O'Connell. 1982. Inshore and shallow offshore bottomfish resources in the southeastern Gulf of Alaska. Alaska Coastal Research, P. O. Box 368, Langley WA, 98260. Final report to State of Alaska, Dep. Fish Game, Comm. Fish. Div. Juneau, 166 p.

[3] Lenarz, W. Tiburon Laboratory, Nat. Mar. Fish. Serv., CA 94920. Personal commun., March 1993.

[4] Barss, B. Marine Science Center, Oregon Dept. Fish. Wildl., Newport, OR 97365. Personal commun., December 1985.

Manuscript accepted 29 November 1993.
Fishery Bulletin 92:655–663 (1994).

ment, studies of blue rockfish, *S. mystinus* (Miller and Geibel, 1973) and olive rockfish, *S. serranoides* (Love, 1980), as well as other studies of yellowtail rockfish (Carlson and Haight, 1972; Pearcy, 1992), indicate much more limited movement. In fact, dispersal from the tagging site was so limited in the latter two studies that the authors hypothesized that yellowtail rockfish have strong homing tendencies and exhibit site fidelity. However, these two studies were conducted over limited spatial and temporal scales.

The purpose of this note is to examine the hypothesis of limited versus extensive movement of yellowtail rockfish. We use data from our two studies, which cover a broader time and space coverage than those studies that implied limited movement. We present the details of the 42 recaptures, discuss some of the factors which may have influenced the overall likelihood of recapture, and conclude with a comment on the management implications of the results.

Table 1

Reports of rockfish, *Sebastes spp.*, movement.

Species	No. of recoveries	Max. dist. moved, (km)	Literature cited
Demersal species			
Black-and-yellow rockfish, *S. chrysomelas*	38	<1	Larson, 1980
Brown rockfish, *S. auriculatus*	22[1]	<1	Matthews et al., 1987
	16	<2	Hartmann, 1987
	1	>50	Lenarz, footnote 3 in text
	11	<2	Gowan, 1983
China rockfish, *S. nebulosus*	13	<1	McElderry, 1979
Copper rockfish, *S. caurinus*	[2]	[2]	Gascon and Miller, 1981
	11[1]	<1	Mathews and Barker, 1983
	29	<1	Matthews et al., 1987
	16	<3	Hartmann, 1987
	75	<3	Gowan, 1983
Gopher rockfish, *S. carnatus*	49	<1	Larson, 1980
Quillback rockfish, *S. maliger*	12	<3	Mathews and Barker, 1983
	28[1]	<1	Matthews et al., 1987
Yelloweye rockfish, *S. ruberrimus*	7	<1	Coombs, 1979
	3	<1	O'Connell, 1991
Semi-pelagic species			
Black rockfish, *S. melanops*	61	<1	McElderry, 1979
	40	<50	Gowan, 1983
	8	400	Mathews and Barker, 1983
	484	555	Culver, 1987
	9	619	Coombs, 1979
Blue rockfish, *S. mystinus*	168	24	Miller and Geibel, 1973
	98	43	Hartmann, 1987
Bocaccio *S. paucispinis*	66	148	Hartmann, 1987
Olive rockfish, *S. serranoides*	435	<33	Hartmann, 1987
Vermilion rockfish, *S. miniatus*	1	10	Turner et al., 1969
Yellowtail rockfish, *S. flavidus*	76	<23	Carlson and Haight, 1972
	10	144	Mathews and Barker, 1983
	25	<4	Pearcy, 1992

[1] Repeated dive observations of tagged fish.
[2] Tagged fish showed strong site fidelity, no numbers provided.

Methods

Methodology used in the Canadian program, which was conducted from 1980 to 1982, has been described in detail (Shaw et al., 1981). The primary area of tagging was off southwest Vancouver Island; additional tagging was performed in Queen Charlotte Sound (Figs. 2 and 3). Fish were captured by trawl at depths of 70–80 m over bottom depths of 110–130 m. Prior to tagging, all fish were anaesthetized with tricaine methanesulphonate (MS-222). Fish with hyperinflated swim bladders were deflated with a hypodermic needle to remove excess gas (Gotshall, 1964), measured to the nearest cm (fork length), and tagged with an external Floy anchor tag imbedded in the dorsal musculature between the pterygiophores. Most fish were injected with oxytetracycline (OTC) (50 mg/kg body wt.) (Leaman and Nagtegaal, 1987). All fish were held for one hour in covered tanks with a continuous flow of seawater. Fish from the last haul of each day were held overnight. Condition after tagging and after release was assessed by using a numerical index based on several categories of injuries (Shaw et al., 1981). We did not record sex of released specimens but did examine

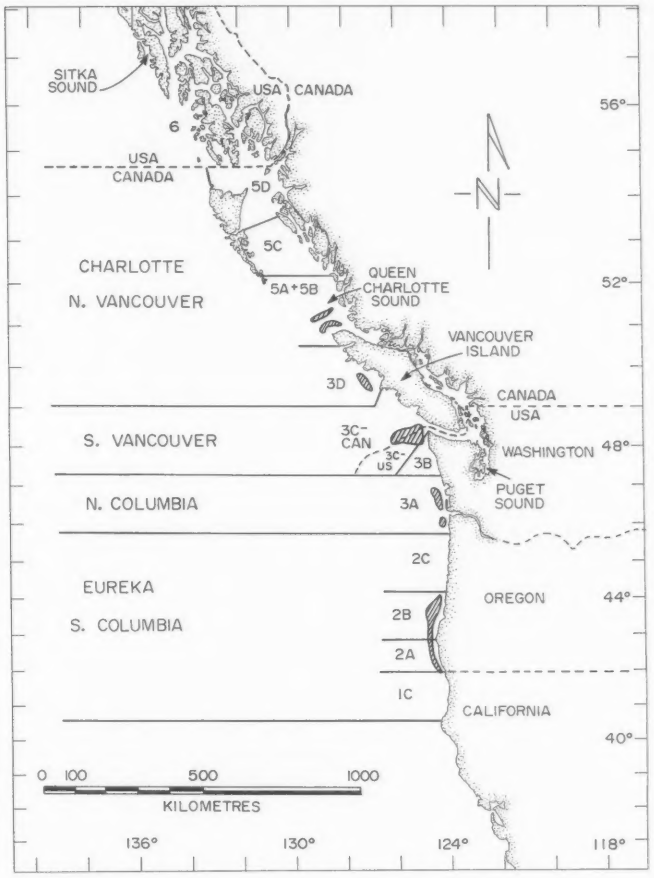


Figure 1

Sites of major yellowtail rockfish, *Sebastes flavidus*, fishing grounds (hatched areas); stock designations are based on individual or combinations of International North Pacific Fishery Commission (INPFC) statistical areas (ie. N. Columbia) and Pacific States Marine Fishery Commission (PSMFC) statistical boundaries within the INPFC areas (ie. 3C-US).

two samples of 100 fish sacrificed during the 1980 tagging off the southwest coast of Vancouver Island.

In the Alaskan program of 1981 and 1982, fish were caught by hook and line from depths of 40–100 m with commercial jigging machines. Fish were examined for decompression stress and hooking damage. Only those fish with no visible stress symptoms were tagged. A total of 397 yellowtail rockfish were tagged as in the Canadian study, but none was injected with OTC or decompressed. All fish were captured and released in July 1982 at two sites in Sitka Sound, Alaska (Fig. 2).

All tag recoveries from both programs were obtained from commercial fisheries. Data on gender and recovery location were obtained when possible, although the latter information was usually limited to statistical area. We calculated the minimum possible distance travelled by assuming the fish travelled a direct course approximating the edge of the continental shelf. Distance was calculated to the border of the statistical area closest to the point of release and rounded down to the nearest 25-km interval. Transit time was calculated as the overall distance divided by the number of days at large. The recovery

ratios (number recovered divided by number released) for the two studies were compared with a two-tailed test of binomial proportions (Kalbfleisch, 1976). We used maturity ogives from Tagart (1991) to infer the proportion mature for specific lengths. He reported 50% maturity at 39.6 cm and 45.4 cm for males and females, respectively, for fish from northern Washington.

We conducted a linear regression of the natural log of number recovered against time (0.5 years–9.5 years) for the Canadian releases to derive a point estimate of the instantaneous annual rate of extinction.

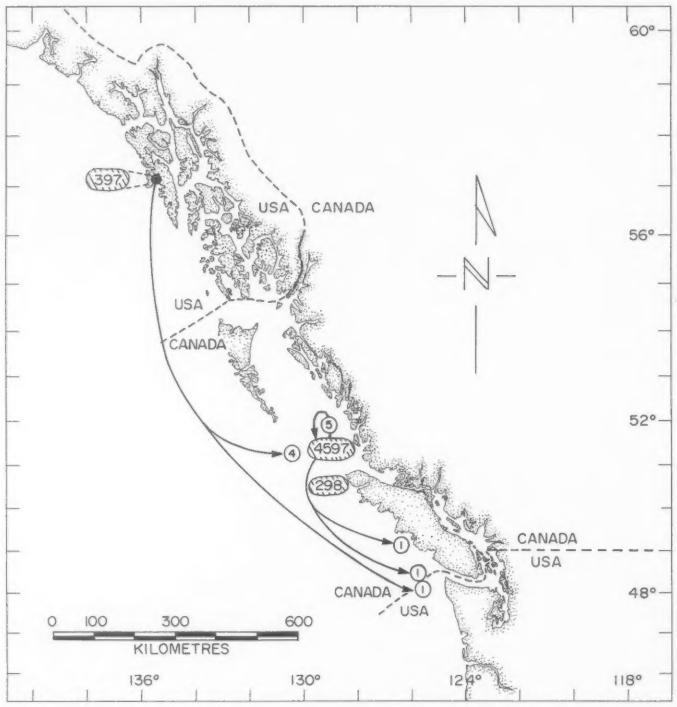


Figure 2

Number of releases (in hatched areas) and recoveries (in circles) of yellowtail rockfish, *Sebastes flavidus,* tagged in southeast Alaska and Queen Charlotte Sound.

Results

Canadian-tagged fish

The Canadian program tagged and released 4,895 fish off central British Columbia (B.C.) and 9,557 off southern B.C. and northern Washington waters. Thirty-seven have been recovered, all from commercial catches from Oregon, Washington, and B.C. waters (Figs. 2 and 3; Table 2). Of these, 36 were accompanied by reliable information on recapture location. Twenty-seven of the 36 (75%), moved less than or equal to 25 km from the release location. However, among the nine fish that travelled more than 25 km, three moved at least 100 km, three others at least 125 km, and one at least 250 km. The farthest displacements of Canadian-tagged fish were one fish that moved from Queen Charlotte Sound to the southwest coast of Vancouver Island (400 km) and one that moved from southwest Vancouver Island to southern Oregon (400 km). The most rapid movements from original tagging sites were two recoveries of Canadian-tagged fish that moved from the north coast of Washington to northern Oregon. One travelled at least 100 km in 73 days (1.37 km/day) whereas the other travelled at least 125 km in 100 days (1.25 km/day).

Average fork length of Canadian-tagged fish was 44.5 cm (23–58 cm). Recovered specimens averaged 45.9 cm (33–54 cm). Among the 21 recoveries for which sex was known, only two were probably immature at the time of release, based on their sex and lengths. Among the nine individuals that travelled further than 25 km, we know the sex of seven. Of these, only one, a 33-cm male, was likely to have been immature at the time of release.

The rate of recoveries from the Canadian study gradually declined over time (Table 3). The point estimate of the instantaneous annual rate of extinction was 0.2. However, the 95% confidence range (0.099–0.307) was wide, reflecting the low number of recoveries.

Alaskan-tagged fish

Of the 397 yellowtail rockfish tagged in Alaska, five have been recovered. All five travelled south to B.C. or to Washington waters over distances of 425–1400 km. The fish were tagged in 1982 but were not recovered until at least 1987. Time at liberty ranged from 1,827 to 2,842 days. The opportunity for recovery of yellowtail rockfish in southeastern Alaska commercial fisheries was limited. The total reported commercial catch in 1991 was three tons; the sport catch was negligible.[5] However, the recovery ratio of Alas-

[5] O'Connell, V. Alaska Dept. Fish Game, Sitka, AK 99835. Personal commun., February 1991.

Table 2

Recoveries of tagged yellowtail rockfish, *Sebastes flavidus*, by the Department of Fisheries and Oceans, Canada, and the University of Alaska; Figure 1 indicates Pacific States Marine Fish Commission Areas (PSMFC); "—" indicates that no information was obtained.

PSMFC area of tagging	PSMFC area of recovery	Days at liberty	Minimum distance displaced (km)	Length at release (cm)	Length at recovery (km)	Injuries at release	Age at recovery (yr)	Sex
Canadian								
3C-US	3B	838	0	44	44	none	15	—
3C-US	3C-US	>3,617	0	44	45	none	—	M
3C-US	3A-3D[1]	N/A	N/A	54	N/A	none	—	—
3C-US	3A	859	125	51	53	none	15	F
3C-US	3C-US	2,577	0	54	N/A	none	—	—
3C-US	3C-US	48	0	53	53	none	—	—
3C-US	3C-US	434	25	46	N/A	bleeding[2]	—	—
3C-US	3C-US	55	0	52	54	none	—	—
3C-US	3C-US	382	0	45	N/A	none	—	—
3C-US	3C-US	2,268	0	45	49	none	—	M
3C-US	3C-US	18	0	43	48	none	—	—
3C-US	4A	1,392	25	45	48	none	—	—
3C-US	3C-US	478	25	47	N/A	none	—	—
3C-CAN	3A	832	125	45	45	loss of scales	13	F
5A+5B	3C-US	1,279	400	42	43	bleeding[3]	11	M
5A+5B	5A+5B	861	25	45	46	none	13	M
5A+5B	3D	3,215	250	42	43	none	—	M
5A+5B	5A+5B	2,119	0	44	48	bleeding[4]	—	M
5A+5B	5A+5B	328	25	46	45	none	20	M
5A+5B	5A+5B	3,219	0	48	48	none	—	M
5A+5B	5A+5B	624	0	51	50	loss of scales	17	M
3C-US	3C-?	1,177	0	49	48	none	—	—
3C-US	2B	690	400	48	45	none	9	F
3C-US	3C-US	73	0	47	N/A	none	—	—
3C-US	3A	798	100	33	39	none	—	M
3C-US	3B	1,218	0	41	46	none	—	M
3C-US	3B	186	0	42	41	none	—	M
3C-US	3A	73	100	46	46	none	—	—
3C-US	3C-US	1,472	0	47	47	none	—	M
3C-US	3A	1,994	100	46	N/A	none	—	—
3C-US	3B	739	0	47	46	none	34	M
3C-US	3C-US	877	0	50	51	none	17	F
3C-US	3C-US	N/A	25	41	39	bruised	—	—
3C-US	3B	1,231	0	48	N/A	none	—	—
3C-US	3C	2,653	0	42	49	none	—	F
3C-US	3A	103	125	42	42	none	—	M
4A	3B	2,438	0	43	46	none	—	M
Alaskan								
SE Alaska	5A+5B	1,827	700	37	45	—	—	—
SE Alaska	3B	2,047	1,400	37	45	—	—	—
SE Alaska	5A+5B	2,842[5]	750	32	N/A	—	—	—
SE Alaska	5A+5B	2,722[6]	625	33	45	—	—	M
SE Alaska	5A+5B	2,729[7]	N/A	41	50	—	—	F

[1] Recovered from Area 3A, 3B, 3C, or 3D.
[2] Bleeding at tag site.
[3] Bleeding at de-gassing site.
[4] Bleeding at oxytetracycline injection site.
[5] 2,842–2,872 days at liberty.
[6] 2,722–3,087 days at liberty.
[7] 2,729–3,094 days at liberty.

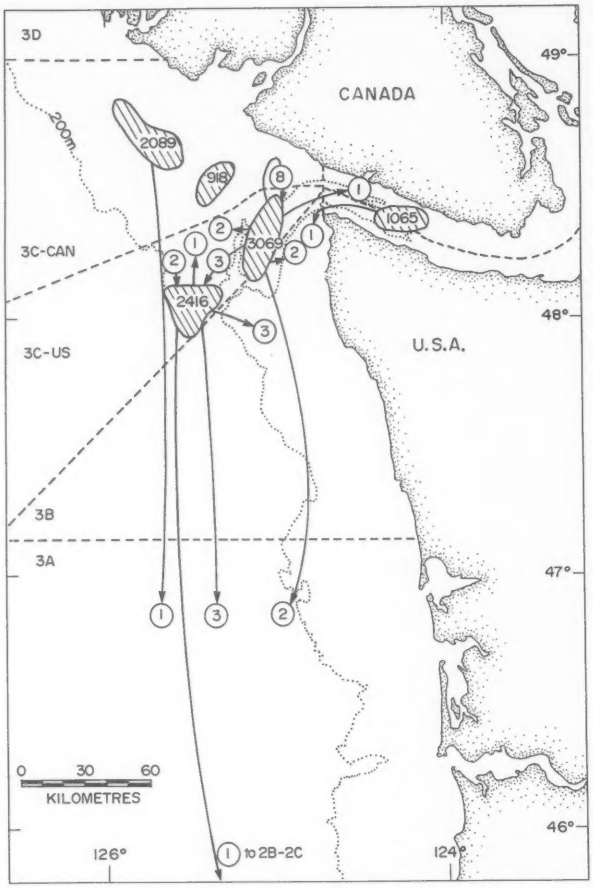


Figure 3

Number of releases (in hatched areas) and recoveries (in circles) of yellowtail rockfish, *Sebastes flavidus*, tagged off southern Vancouver Island and northern Washington (one specimen released in PSMFC area 3C-US was recovered in Areas 2B–2C to the south of the areas shown in this figure).

kan specimens (1.3%) was significantly higher ($P<0.05$) than in the Canadian study (0.26%), even without significant commercial fisheries in the area of release. The average length of all Alaskan-tagged fish was 37 cm (22–56 cm). The average length of recovered fish was 46 cm (45–50 cm). Based on the lengths, the recovered specimens were probably sexually mature when recovered, but probably immature when released.

Discussion

The recoveries of Alaskan specimens are congruent with earlier work, which indicated that immature yellowtail rockfish can make long distance movements (Mathews and Barker, 1983). The Canadian recoveries provide the first evidence that mature yellowtail rockfish can also move significantly longer distances than has been previously reported (Carlson and Haight, 1972; Pearcy, 1992).

The consistent tendency for individuals who travelled away from the release points to be caught farther south along the coast probably resulted from the bias in the distribution of the fishing effort. For the Alaskan and central B.C. releases, there were virtually no fisheries north or west of the release areas. It is surprising that none of the fish tagged in northern

Washington were recovered in Queen Charlotte Sound. However, landings of yellowtail rockfish in Queen Charlotte Sound were also low in the years during, and the first three years following, tagging (Table 4).

The yellowtail rockfish tagged in the Alaskan study were caught in waters shallower than 30 m and were predominantly immature. A southward, ontogenetic migration to the broader continental shelf off central B.C. is possible. This would parallel the movement of immature yellowtail rockfish from Puget Sound to the outer Washington coast (Mathews and Barker, 1983). However, many of these fish may simply move west towards the deeper water on the outer shelf but remain within southeastern Alaska. The limited commercial fishery in these outside waters prevents resolution of these alternatives, although they are not mutually exclusive.

We suggest that the low recovery rate for the Canadian study was caused by short-term post-tagging mortality arising from a combination of the greater depth of capture, the greater stress from trawl capture compared with hook-and-line, and the added handling during anaesthetization, decompression, and OTC injection. The dosage level of OTC may have also contributed to mortality, as studies on other species have shown increasing mortality with dosages greater than 25 mg/kg body weight (McFarlane and Beamish, 1987).

An alternative explanation for low recovery rates in the Canadian study is that the tagged fish were released into very large populations, well in excess of current estimates (Table 4). Thus, landings of 400–900 t in the early 1980's provided little chance for recovery. However, this same logic should then apply to the likelihood of recapturing Alaskan tags in the B.C. fishery at the same time. Since this recovery ratio was much higher, the Alaskan results support the contention of high initial mortality in the Canadian study.

The rate of recovery for Canadian tags was low at the outset and gradually declined over the ten years after release. The 95% confidence limits of the point estimate for the instantaneous rate of decline over the ten years (0.099–0.307) is consistent with the range of extinction rates (0.28–0.54) predicted by combining published estimates of instantaneous rates for natural mortality, 0.06–0.12 (Archibald et al., 1981; Tagart, 1991), tag loss for black rockfish, 0.13 (Lai and Culver, 1991), and fishing mortality for yellowtail rockfish off northern Washington, 0.09–0.29 (Tagart, 1991).

Despite the commercial importance of this species, the stock boundaries are poorly understood. Assessment biologists have resorted to selecting boundaries based on a combination of official statistical areas and on the distribution of major fishing grounds. The most recent assessments have assumed four stocks from groupings of International North Pacific

Table 3

Minimum estimate of years at liberty for yellowtail rockfish, *Sebastes flavidus*, tag recoveries for those with reliable information on recovery date.

Time at liberty (yr)	Number of recoveries	
	Canadian	Alaskan
<1	8	0
1–2	5	0
2–3	7	0
3–4	5	0
4–5	1	0
5–6	2	2
6–7	2	0
7–8	2	3
8–9	2	0
9+	1	0
Total	35	5

Table 4

Landings (t) for 1980–89 and biomass estimates (t) for 1990 of yellowtail rockfish, *Sebastes flavidus*, by region (Stanley, 1991; Tagart, 1991).

Year of landings	SE Alaska	British Columbia[1]	Washington-Oregon-California[2]
1980		704	8,667
1981		426	9,181
1982	1	526	9,184
1983	2	447	9,498
1984	6	353	5,392
1985	5	941	3,449
1986	5	4,458	5,082
1987	8	4,168	5,212
1988	6	4,765	6,193
1989	4	4,298	4,516
1990 Exploitable biomass	unknown	30,000–45,000	20,000–40,000

[1] Northern Vancouver stock biomass partitioned 50% to Washington, 50% B.C.
[2] Does not include the bycatch in offshore fishing for Pacific hake, *Merluccius productus*.

Fisheries Commission statistical areas: Charlotte/North Vancouver, South Vancouver, North Columbia, and Eureka/South Columbia (Stanley, 1991; Tagart, 1991) (Fig. 1).

This study does not provide information sufficient to alter the boundaries presently used in stock assessments. However, the clear demonstration of movement for immature and mature yellowtail rockfish should encourage assessment biologists to refine their understanding of stock relationships for this species. This understanding can then be applied to examination of the relative impacts of fishing mortality and potential movements among stock units.

Acknowledgments

The Alaskan tagging program could not have been accomplished without the expertise and assistance of L. J. Field, M. LaRiviere, and especially Richard Rosenthal. We also appreciate the review comments of Bill Pearcy and two anonymous reviewers.

Literature cited

Archibald, C. P., W. Shaw, and B. M. Leaman.
1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. Can. Tech. Rep. Fish. Aquat. Sci. 1048, 57 p.

Carlson, R. H., and R. E. Haight.
1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29:1011–1014.

Coombs, C.
1979. Reef fishes near Depoe Bay, Oregon: movement and the recreational fishery. M.A. thesis, Oregon State Univ., Corvallis, 39 p.

Culver, B. N.
1987. Results from tagging black rockfish (*Sebastes melanops*) off the Washington and northern Oregon coast. *In* Proceedings of the international rockfish symposium, p. 231–239. Univ. Alaska Sea Grant Rep. 87-2. Univ. Alaska, Fairbanks, 393 p.

Fadeev, N. S.
1968. Migrations of Pacific ocean perch. Proc. Pac. Sci. Res. Inst. Fish. Ocean. 65:170–177. [Fish. Res. Board Can. Transl. Ser. 1447.]

Gascon, D., and R. A. Miller.
1981. Colonization by nearshore fish on small artificial reefs in Barkley Sound, British Columbia. Can. J. Zool. 59:1635–1646.

Gotshall, D. W.
1964. Increasing tagged rockfish (genus *Sebastodes*) survival by deflating the swim bladder. Calif. Dep. Fish Game, Fish. Bull. 50:253–260.

Gowan, R. E.
1983. Population dynamics and exploitation rates of rockfish (*Sebastes* spp.) in central Puget Sound, Washington. Ph.D. thesis, Univ. Wash., Seattle, 90 p.

Gunderson, D. R.
1971. Evidence that Pacific ocean perch (*Sebastes alutus*) in Queen Charlotte Sound form aggregations that have different biological characteristics. J. Fish. Res. Board Can. 29:1061–1070.

Hartman, A. R.
1987. Movement of scorpionfishes (Scorpaenidae: *Sebastes* and *Scorpaena*) in the southern California Bight. Calif. Dep. Fish Game, Fish. Bull. 73(2):68–79.

Kalbfleisch, J. G.
1976. Probability and statistical inference, Part 2. Univ. Waterloo, Waterloo, Ontario, 307 p.

Lai, H., and B. N. Culver.
1991. Estimation of tag loss rate of black rockfish (*Sebastes melanops*) off the Washington coast with a review of double tagging models. Wash. Dept. Fish. Tech. Rep. 113, 28 p.

Larson, R. J.
1980. Territorial behaviour of the black-and-yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). Mar. Biol. 58:111–122.

Leaman, B. M., and Z. Kabata.
1987. *Neobrachiella robusta* (Wilson, 1912) (Copepoda:Lernaepodidae) as a tag for identification of stocks of its host, *Sebastes alutus* (Gilbert, 1890) (Pisces:Teleostei). Can. J. Zool. 65:2579–2582.

Leaman, B. M., and D. A. Nagtegaal.
1987. Age validation and revised natural mortality rate for yellowtail rockfish. Trans. Am. Fish. Soc. 116:171–175.

Love, M. S.
1980. Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. Fish. Bull. 77:975–983.

Mathews, S. B., and M. W. Barker.
1983. Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. Fish. Bull. 81:916–922.

Matthews, K. R., B. S. Miller, and T. P. Quinn.
1987. Movement studies of nearshore demersal rockfishes in Puget Sound, Washington. *In* Proceedings of the international rockfish symposium, p. 63–72. Univ. Alaska Sea Grant Rep. 87–2. Univ. Alaska, Fairbanks, 393 p.

McElderry, H. I.
1979. A comparative study of the movement habits and their relationships to buoyancy compensation in two species of shallow reef rockfish (Pisces: Scorpaenidae). M.Sc. thesis, Univ. Victoria, Victoria, B.C., 168 p.

McFarlane, G. A., and R. J. Beamish.
1987. Selection of dosages of oxytetracycline for age validation studies. Can. J. Fish. Aquat. Sci. 44(4):905–909.

Miller, D. J., and J. J. Geibel.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera,* experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

O'Connell, V. M.
1991. A preliminary examination of breakaway tagging for demersal rockfishes. Alaska Dep. Fish Game, Comm. Fish. Div., Fish. Res. Bull. 91-06, 8 p.

Pearcy, W. G.
1992. Movements of acoustically-tagged yellowtail rockfish *Sebastes flavidus* on Heceta Bank, Oregon. Fish. Bull. 90:726–735.

Shaw, W., D. A. Nagtegaal, C. P. Archibald, and B. M. Leaman.
1981. Rockfish tagging cruises off southwest Vancouver Island (MV *Ocean King*) and off northwest Vancouver Island and in Queen Charlotte Sound (MV *Blue waters*) during 1980. Can. Data Rep. Fish. Aquat. Sci. 288, 133 p.

Stanley, R. D.
1991. Shelf rockfish (silvergray, yellowtail, canary rockfish). *In* J. Fargo, and B. M. Leaman (eds.), Groundfish stock assessments for the west coast of Canada in 1990 and recommended yield options for 1991, p. 225–276. Can. Tech. Fish. Aquat. Sci. 1778.

Tagart, J. V.
1991. Population dynamics of yellowtail rockfish *Sebastes flavidus* stocks in the northern California to southwest Vancouver Island Region. Ph.D. thesis, Univ. Wash., Seattle, 323 p.

Turner, C. H., E. E. Ebert, and R. R. Given.
1969. Man-made reef ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.

Wishard, L. N., F. M. Utter, and D. R. Gunderson.
1980. Stock separation of five rockfish species using naturally occurring biochemical markers. Mar. Fish Rev. 42:64–73.

A simple generalized model of allometry, with examples of length and weight relationships for 14 species of groundfish

Yongshun Xiao

David C. Ramm

Fisheries Division, Department of Primary Industry and Fisheries
GPO Box 990, Darwin NT 0801, Australia

Allometry is a set of relations between an animal's characteristics and its body size, and is applied in many branches of biological sciences including ecology, physiology, and morphology (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Bookstein et al., 1985; Reiss, 1989). Allometry is represented by the power function, $W = AL^{X_2}$, where W is a characteristic of an animal (e.g. body weight), L is its body size, and A and X_2 are its allometric parameters. To determine an allometric relationship for a particular characteristic, the power function is usually, albeit at times inappropriately, double log-transformed into a simple linear equation,

$$Y = X_1 + X_2 X_3, \qquad (1)$$

with $Y = \log(W)$, $X_1 = \log(A)$, and $X_3 = \log(L)$, and is then fit to data from different individuals.

Use of allometry in this way assumes constancy of X_1 and X_2 in Equation 1. While both allometric parameters may be treated approximately as constants in certain applications, the assumption may be violated for a wide variety of biological phenomena because of genetic, phenotypic, and/or behavioral variability among individual animals. In fact, Mosimann and James (1979) have concluded that X_2 varies spatially in the Florida red-winged blackbird, *Agelaius phoeniceus*. Variability in X_2 is also implied in Reiss' (1989) hypothesis that X_2 contains phylogenetic information and is less variable intraspecifically than interspecifically. Peters (1983) convincingly demonstrated interspecific variation in X_2 and computed its mean and standard deviation for metabolic rates scaled to body sizes across many animal taxa. Variability in X_1 has not been examined but is certainly implied in the comprehensive appendices of Peters' (1983) book on the ecological implications of body size and in Reiss' (1989) monograph on the allometry of organismic growth and reproduction. X_1 may be strongly negatively correlated with X_2 for length-weight relationships in fish (e.g. Caillouet, 1993).

Variability in X_1 and X_2 may have major implications in the widely used allometric equation because it represents a fundamental concept in biology (Peters, 1983). In this paper, we generalize Equation 1 by explicitly incorporating variability in and correlation between, X_1 and X_2, and study the consequences of such variability and correlation in allometric predictions. The generalized model is demonstrated by using length and weight relationships for 14 species of groundfish of the families Centrolophidae, Haemulidae, Lethrinidae, Lutjanidae, Nemipteridae, and Synodontidae from northern Australian waters.

Model

Suppose that a joint probability distribution of X_1 and X_2 conditional on X_3 could be formed for a group of animals, with each individual having its own pair of allometric parameters which it retains throughout its life, and that values of pairs of allometric parameters are serially independent. The value of Y for the ith individual with allometric parameter pair (X_{1i}, X_{2i}) at X_3 is

$$Y_i = X_{1i} + X_{2i} X_3.$$

For a group of animals selected randomly from the population, the expected value of Y at X_3 is

$$E[Y \mid X_3] = E[X_1 + X_2 X_3] \qquad (2)$$

with variance

$$\begin{aligned} V[Y \mid X_3] &= V[X_1 + X_2 X_3] \\ &= E[Y^2 \mid X_3] - E[Y \mid X_3]^2 \\ &= E[(X_1 + X_2 X_3)^2] - E[X_1 + X_2 X_3]^2. \end{aligned} \qquad (3)$$

Given information on how X_1 and X_2 vary, one can develop Equations 2 and 3. X_2 may closely follow a normal distribution for metabolic rate of animals scaled to body size (Peters, 1983), being strongly negatively correlated with X_1 for length-weight relationships in fish (e.g. Caillouet, 1993). We will assume below that X_1 and X_2 follow a joint normal distribution, i.e. $(X_1, X_2) \sim N(\mu_1, \mu_2; \sigma_1^2, \sigma_2^2; \rho)$ with mean μ_i, and variance σ_i^2 of X_i, and correlation coefficient ρ. Under general conditions, the sum (or average) of a number of random variables is approximately normally distributed, and such approximation can be quite good even if that number is relatively small. The above assump-

Manuscript accepted 25 February 1994.
Fishery Bulletin 92: 664–670 (1994).

tion would be at least approximately valid because both X_1 and X_2 can be regarded as the sum (or average) of numerous (e.g. genetic, phenotypic, and behavioral) random components. Analogous models may be developed for other probability distributions. Under that assumption, Equations 2 and 3 become, respectively,

$$\begin{aligned} E[Y \mid X_3] &= E[X_1 + X_2 X_3] \\ &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \frac{1}{2\pi\sigma_1\sigma_2\sqrt{1-\rho^2}} (x_1 + x_2 X_3) e^{-\frac{1}{2(1-\rho^2)}\left[\frac{(x_1-\mu_1)^2}{\sigma_1^2} - 2\rho\frac{(x_1-\mu_1)(x_2-\mu_2)}{\sigma_1\sigma_2} + \frac{(x_2-\mu_2)^2}{\sigma_2^2}\right]} dx_1 dx_2 \\ &= \mu_1 + \mu_2 X_3, \end{aligned} \tag{4}$$

and

$$\begin{aligned} V[Y \mid X_3] &= V[X_1 + X_2 X_3] \\ &= E[Y^2 \mid X_3] - E[Y \mid X_3]^2 \\ &= E[(X_1 + X_2 X_3)^2] - E[X_1 + X_2 X_3]^2 \\ &= \sigma_1^2 + 2\sigma_1\sigma_2\rho X_3 + \sigma_2^2 X_3^2. \end{aligned} \tag{5}$$

Thus variability in, and correlation between, X_1 and X_2 only affect $V[Y \mid X_3]$. $V[Y \mid X_3]$ increases linearly with ρ from $(\sigma_1 - \sigma_2 X_3)^2$ at $\rho = -1$ through $\sigma_1^2 + \sigma_2^2 X_3^2$ at $\rho = 0$ to $(\sigma_1 + \sigma_2 X_3)^2$ at $\rho = 1$. It quadratically decreases with σ_1, σ_2, and X_3 to a minimum of $\sigma_2^2 X_3^2 (1-\rho^2) \geq 0$ at $\sigma_1 = -\sigma_2\rho X_3$, $\sigma_1^2(1-\rho^2)$ at $\sigma_2 = -\sigma_1\rho / X_3$ and $\sigma_1^2(1-\rho^2)$ at $X_3 = -\sigma_{1\rho}/\sigma_2$, respectively, and finally increases unboundedly, under the constraint that σ_1, σ_2, and $X_3 \geq 0$. However, if X_1 and X_2 are both deterministic ($\sigma_i^2 = 0, \rho = 0$), $V[Y \mid X_3] = 0$.

If X_1 is random ($\sigma_1^2 > 0$) and X_2 is deterministic ($\sigma_2^2 = 0, \rho = 0$), $V[Y \mid X_3] = \sigma_1^2$. If X_2 is random ($\sigma_2^2 > 0$) and X_1 is deterministic ($\sigma_1^2 = 0, \rho = 0$), $V[Y \mid X_3] = \sigma_2^2 X_3^2$. Finally, if X_1 and X_2 are random but independent ($\sigma_1^2 > 0, \sigma_2^2 > 0$ and $\rho = 0$), $V[Y \mid X_3] = \sigma_1^2 + \sigma_2^2 X_3^2$.

Data and parameter estimation

Data on fish weight at length were collected from Australia's continental shelf in the Timor and Arafura Seas (9–14°S, 127–137°E) from 20 October to 16 December 1990 as part of the Northern Territory Department of Primary Industry and Fisheries' program assessing commercial fish stocks. Of 240 stations allocated randomly within a depth range of 20–200 m, 199 were successfully sampled with a Frank and Bryce trawl net (headline height, 2.9 m; wing spread, 14.4 m; door spread, 60.1 m) at a speed of 1.54–2.06 $m \cdot s^{-1}$. Nearly 48 tonnes of fish representing about 483 species in 119 families were caught during sampling. A representative subsample of individuals of 14 species, mostly of commercial fish, of the families Centrolophidae, Haemulidae, Lethrinidae, Lutjanidae, Nemipteridae, and Synodontidae were frozen immediately on board, returned to the laboratory, thawed, sexed, measured (fork length) to the nearest 1 mm, and weighed (wet weight) to the nearest 1 g with an electronic balance (Mettler, PC4000). For each of the 14 species, data on individual wet weight at length were pooled across all stations and fit to all cases of Equations 4 and 5 for females, males, and mixed sexes. Parameter estimates indicated by hats (^) were obtained by linear regression for Equation 1 by using SAS regression procedure (SAS Institute Inc., 1985) and by maximizing the general likelihood function,

$$L = \prod_{i=1}^{n} \left[2\pi V[Y \mid X_3] + \sigma_e^2\right]_i^{-\frac{1}{2}} e^{-\frac{[Y_i - E[Y \mid X_3]_i]^2}{2\left[V[Y \mid X_3]_i + \sigma_e^2\right]}},$$

for all other models by using the simplex algorithm of SYSTAT nonlinear regression procedure (Wilkinson, 1989). We included a model error term, σ_e^2, in the likelihood function to show that, in this case, it is compounded with σ_1^2 and is hence equivalent to σ_1^2 and $\sigma_1^2 + \sigma_e^2$ for estimation purposes. For this reason, we treated both error components collectively as 'σ_1^2' during model fitting and result presentation, unless otherwise stated.

Results

Some statistics of fish length and weight data used in this analysis are given in Table 1. We attempted to fit data for mixed sexes (both sexable and unsexable individuals included) and males and females (with unsexable juveniles excluded) of each of 14 species of groundfish to all cases of Equations 4 and 5. However, parameters could be estimated for models with σ_1^2 or σ_2^2 only; those in models simulta-

neously with σ_1^2 and σ_2^2, or simultaneously with σ_1^2, σ_2^2 and ρ could not be estimated because of overparameterization. Estimates of parameters, derived from linear regression of Equation 1 by using least squares method—equivalent to maximizing the likelihood function

$$L = \prod_{i=1}^{n} \left[2\pi\sigma_1^2\right]^{-\frac{1}{2}} e^{-\frac{[Y_i - E[Y|X_3]_i]^2}{2\sigma_1^2}}$$

and from maximizing the likelihood function

$$L = \prod_{i=1}^{n} \left[2\pi\sigma_2^2 X_3^2\right]^{-\frac{1}{2}} e^{-\frac{[Y_i - E[Y|X_3]_i]^2}{2\sigma_2^2 X_3^2}},$$

are given in Tables 2 and 3 respectively. Estimates in both tables are very similar between sexes for each species and between species, roughly with a species-wide $\hat{\mu}_1 = -10.89$, $\hat{\mu}_2 = 2.99$, $\sigma_1 = -0.006638$ and $\hat{\sigma}_2 = 0.014932$. Thus, while $V[Y|X_3]$ can be treated approximately as a constant, as is usually assumed in previous applications, it does change quadratically with X_3.

Discussion

Peters (1983) observed a large amount of variability in most allometric relationships and recognized a need to identify independent variables of general biological interest other than size. The general model presented in this study takes into account both body size and parameter variability among individual animals in allometric predictions. A major problem in allometry is that allometricians are more apt at providing a statistical description of a new data set than at using their data for hypothesis testing (Peters, 1983). This tendency has led to a plethora of only slightly different allometric equations, none of which can be rejected objectively. Our general model or any of its special cases would form a basis for intrataxal or intertaxal generalizations by treating some of those estimates of allometric parameters as intrataxal or intertaxal variations, hence providing a means for a general "house cleaning" in allometry.

Incorporating more independent variables in allometric modelling may explain more variability in the dependent variable, but it may result in a loss of a basis for comparison between, and manipulation of, allometric equations, such as allometric cancellation (Calder, 1984). The model presented above conforms exactly with conventional allometry and maintains commensuration by its estimated parameter means.

Specification of error structures in allometric models is an essential part of allometric modelling. Errors for Equation 1 are often assumed to be normally distributed with a constant variance, say σ_e^2. Several other interpretations arise from $V[Y|X_3]$ in that, for estimation purposes, σ_e^2 can be interpreted by any combinations of terms on the right-hand side of Equation 5. These and other alternative interpretations may pose problems for some applications. Thus, error structures of an allometric model must be specified cautiously.

There was no gain in precision or accuracy in estimates of allometric parameters in length and weight relationships of some fishes from considering individual variability of allometric parameters. Both Equation 1 and Equations 4 and 5 with σ_1^2 or σ_2^2, alone give an equally adequate description of weight at length data from all 14 species of groundfish concerned. Overparameterization occurred in cases of Equations 4 and 5 simultaneously with σ_1^2 and σ_2^2, or simultaneously with σ_1^2, σ_2^2, and ρ, and, as a result, not all parameters could be estimated from our data. The overparameterization lent further support to this conclusion. Also, although σ_1^2 and σ_2^2 can be estimated separately for each species, they are either equivalent to model error or take such small values (Tables 2 and 3) that $V[Y|X_2]$ can be treated effectively as constant. Finally, when interpreting regression results from various cases of the general model, it should be noted that all other variability will be confounded with, and added to, that of allometric parameters. Our data sets are of moderate sizes (Table 1) and many others of similar size could be expected to behave similarly. Individual variability of allometric parameters probably has a negligible effect on allometric predictions in length and weight relationships of certain fishes. Thus, our work supports the common use of Equation 1 to model intraspecific length and weight relationships in those fishes. However, all parameters in Equations 4 and 5 may be estimable simultaneously for length and weight relationships, as well as for other allometric relationships, if larger data sets or higher taxonomic levels, or both, are used.

A key assumption in our model is that the independent characteristic, L, (e.g. length) has little measurement error relative to the dependent characteristic, W (e.g. weight). Theoretically, this may not be the case. However, we believe that our model will provide good approximations for many allometrically scaled phenomena, such as length and weight relationships in certain fishes. For other allometric phenomena, alternative formulations, such as those of Pienaar and Ricker (1968), Saenger (1989), Seim and Saether (1983), and Shoesmith (1990) may be useful.

$V[Y|X_3]$ is a function of the independent variable whenever there is individual variability in X_2 or in X_1 and X_2. If this is not taken into account in regres-

Table 1

Some statistics of length and weight data for mixed sexes (both sexable and unsexable individuals included), males and females (with unsexable juveniles excluded) of each of 14 species of groundfish caught in northern Australian waters during 20 October to 16 December 1990.

			Fork length (mm)				Body weight (g)			
Sex	Species	*n*	Mean	SD	Min	Max	Mean	SD	Min	Max
Mixed										
Diagramma pictum	painted sweetlip	413	374.753	135.174	127	610	1,044.94	906.31	27	3,415
Lethrinus fraenatus	blue-lined emperor	48	344.562	63.134	201	450	907.77	469.80	165	1,837
Lethrinus lentjan	red-spot emperor	334	278.521	43.792	190	430	457.04	234.31	143	1,567
Lutjanus erythropterus	scarlet snapper	172	431.105	54.429	255	536	1,269.63	417.65	255	2,373
Lutjanus malabaricus	saddle-tailed snapper	590	377.398	151.595	86	765	1,170.71	1074.90	13	7,251
Lutjanus sebae	red emperor	182	342.346	125.237	94	596	1,144.50	974.22	18	4,736
Lutjanus timorensis	Timor snapper	43	415.256	38.608	211	453	1,339.72	271.27	178	1,663
Lutjanus vittus	one-band snapper	450	188.364	30.864	98	300	114.65	59.41	15	461
Nemipterus furcosus	rosy threadfin-bream	479	164.382	34.187	38	250	95.61	55.97	3	300
Nemipterus hexodon	ornate threadfin-bream	479	149.714	28.517	93	230	73.35	44.00	15	252
Pristipomoides multidens	gold-band snapper	293	314.055	117.079	131	585	818.53	882.70	50	3,800
Pristipomoides typus	sharp-tooth snapper	131	207.130	106.140	87	550	302.01	540.41	12	2,705
Psenopsis humerosa	black-spot butterfish	254	158.106	14.633	105	195	106.74	32.23	25	202
Saurida micropectoralis	short-finned lizardfish	444	261.218	34.039	110	410	194.26	90.32	12	850
Female										
Diagramma pictum	painted sweetlip	185	405.827	118.834	185	610	1,192.71	847.30	88	3,377
Lethrinus fraenatus	blue-lined emperor	32	318.031	48.035	201	445	690.22	313.06	165	1,757
Lethrinus lentjan	red-spot emperor	255	265.435	35.665	194	422	389.43	185.90	146	1,567
Lutjanus erythropterus	scarlet snapper	78	430.731	43.480	345	536	1,285.32	402.82	627	2,373
Lutjanus malabaricus	saddle-tailed snapper	193	472.637	90.217	175	716	1,702.28	811.06	89	5,196
Lutjanus sebae	red emperor	88	386.159	86.001	197	535	1,357.81	791.64	155	3,176
Lutjanus timorensis	Timor snapper	25	414.520	22.417	378	451	1,320.64	207.65	978	1,663
Lutjanus vittus	one-band snapper	212	181.835	24.025	120	262	100.01	41.03	29	289
Nemipterus furcosus	rosy threadfin-bream	240	161.429	25.781	38	230	85.36	40.47	7	239
Nemipterus hexodon	ornate threadfin-bream	270	146.463	23.825	97	208	67.34	33.01	18	176
Pristipomoides multidens	gold-band snapper	98	356.735	117.750	180	585	1,103.23	1,001.25	108	3,800
Pristipomoides typus	sharp-tooth snapper	29	287.034	111.650	135	550	593.48	720.46	42	2,705
Psenopsis humerosa	black-spot butterfish	101	167.050	12.046	138	195	126.50	30.13	61	202
Saurida micropectoralis	short-finned lizardfish	164	284.860	36.753	197	410	256.20	111.99	71	850
Male										
Diagramma pictum	painted sweetlip	119	448.303	111.902	177	594	1,528.94	917.86	77	3415
Lethrinus fraenatus	blue-lined emperor	16	397.625	56.707	216	450	1,342.88	431.39	191	1837
Lethrinus lentjan	red-spot emperor	74	325.743	35.281	220	430	698.30	229.21	202	1469
Lutjanus erythropterus	scarlet snapper	93	433.312	59.850	258	535	1,267.23	421.10	255	2233
Lutjanus malabaricus	saddle-tailed snapper	200	449.215	122.859	183	765	1,622.40	1,121.62	105	7251
Lutjanus sebae	red emperor	45	423.822	94.510	187	596	1,772.42	1,048.84	124	4736
Lutjanus timorensis	Timor snapper	17	428.353	19.193	388	453	1,436.12	183.58	1,021	1613
Lutjanus vittus	one-band snapper	225	197.858	31.901	128	300	132.84	67.83	32	461
Nemipterus furcosus	rosy threadfin-bream	205	178.800	30.351	115	250	120.09	61.04	28	300
Nemipterus hexodon	ornate threadfin-bream	125	165.832	32.361	107	230	99.21	58.00	20	252
Pristipomoides multidens	gold-band snapper	127	333.276	108.795	141	580	897.81	840.95	60	3,475
Pristipomoides typus	sharp-tooth snapper	35	267.314	99.371	114	530	477.31	581.00	27	2,617
Psenopsis humerosa	black-spot butterfish	117	153.821	13.416	105	191	97.19	26.08	25	198
Saurida micropectoralis	short-finned lizardfish	263	249.433	19.805	186	295	161.19	41.16	63	289

sion analysis, too much weight would be given to observations of the dependent variable in the region with high variances, and the analysis will be overly sensitive to chance events or bias affecting observations in this region of the independent variable.

Length and weight relationships in fishes are often required for stock assessment and for intra- and inter-specific comparisons. Although many data are available on weight at length relationships of fishes from New Guinea (Showers, 1993) and New Cale-

Table 2

Estimates of mean and standard error of allometric parameters obtained for mixed sexes, males, and females of each of 14 species of groundfish, caught in northern Australian waters during 20 October to 16 December 1990 by linear regression of Equation 1 by using least squares method. $P \leq 0.0001$ applies to all species for separate sexes.

	Mixed					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	P	R^2
Diagramma pictum	−11.4249 (0.0650)	3.0427 (0.0111)	411	75,363.608	0.0000	0.9946
Lethrinus fraenatus	−11.1084 (0.2933)	3.0501 (0.0503)	46	3,673.450	0.0001	0.9874
Lethrinus lentjan	−10.8678 (0.1287)	3.0049 (0.0229)	332	17,226.485	0.0001	0.9810
Lutjanus erythropterus	−10.2265 (0.2323)	2.8569 (0.0383)	170	5,550.516	0.0001	0.9701
Lutjanus malabaricus	−10.4713 (0.0478)	2.8926 (0.0082)	588	125,849.921	0.0000	0.9953
Lutjanus sebae	−10.7588 (0.0752)	2.9931 (0.0130)	180	52,732.028	0.0001	0.9966
Lutjanus timorensis	−10.2548 (0.5172)	2.8916 (0.0858)	41	1,134.654	0.0001	0.9643
Lutjanus vittus	−10.5972 (0.0985)	2.9136 (0.0188)	448	23,905.566	0.0000	0.9816
Nemipterus furcosus	−10.6433 (0.1163)	2.9552 (0.0229)	477	16,672.088	0.0000	0.9721
Nemipterus hexodon	−10.8475 (0.1277)	3.0010 (0.0256)	477	13,778.375	0.0000	0.9665
Pristipomoides multidens	−10.4284 (0.0629)	2.9192 (0.0110)	291	69,881.156	0.0000	0.9958
Pristipomoides typus	−10.6474 (0.0672)	2.9462 (0.0128)	129	52,895.132	0.0001	0.9975
Psenopsis humerosa	−11.8119 (0.2644)	3.2487 (0.0523)	252	3,863.670	0.0001	0.9385
Saurida micropectoralis	−12.3581 (0.1948)	3.1560 (0.0351)	442	8,106.551	0.0001	0.9482
	Female					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	R^2	
Diagramma pictum	−11.4854 (0.1323)	3.0526 (0.0222)	183	18,940.693	0.9904	
Lethrinus fraenatus	−10.9359 (0.4586)	3.0204 (0.0797)	30	1,435.635	0.9788	
Lethrinus lentjan	−11.0141 (0.1823)	3.0314 (0.0327)	253	8,591.353	0.9713	
Lutjanus erythropterus	−11.1443 (0.3965)	3.0123 (0.0654)	76	2,120.223	0.9649	
Lutjanus malabaricus	−10.6937 (0.1855)	2.9290 (0.0302)	191	9,397.044	0.9800	
Lutjanus sebae	−10.9484 (0.2014)	3.0256 (0.0339)	86	7,943.456	0.9892	
Lutjanus timorensis	−8.5750 (1.6316)	2.6136 (0.2708)	23	93.182	0.7934	
Lutjanus vittus	−10.4418 (0.1823)	2.8824 (0.0351)	210	6,752.525	0.9697	
Nemipterus furcosus	−9.0380 (0.2490)	2.6379 (0.0491)	238	2,888.362	0.9236	
Nemipterus hexodon	−10.5120 (0.1626)	2.9366 (0.0327)	268	8,081.145	0.9678	
Pristipomoides multidens	−10.4544 (0.1318)	2.9235 (0.0226)	96	16,739.747	0.9942	
Pristipomoides typus	−10.3553 (0.1890)	2.8933 (0.0337)	27	7,358.630	0.9962	
Psenopsis humerosa	−12.0558 (0.5391)	3.2969 (0.1054)	99	978.916	0.9072	
Saurida micropectoralis	−12.4764 (0.3404)	3.1777 (0.0603)	162	2,777.965	0.9446	
	Male					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	R^2	
Diagramma pictum	−11.8373 (0.1399)	3.1102 (0.0230)	117	18,239.181	0.9936	
Lethrinus fraenatus	−11.5601 (0.5382)	3.1252 (0.0901)	14	1,204.055	0.9877	
Lethrinus lentjan	−11.1870 (0.3227)	3.0589 (0.0558)	72	3,002.105	0.9763	
Lutjanus erythropterus	−9.9051 (0.2875)	2.8006 (0.0474)	91	3,487.397	0.9743	
Lutjanus malabaricus	−10.6166 (0.1268)	2.9171 (0.0209)	198	19,525.208	0.9899	
Lutjanus sebae	−11.5487 (0.2166)	3.1216 (0.0359)	43	7,544.416	0.9942	
Lutjanus timorensis	−9.4597 (1.8694)	2.7597 (0.3085)	15	80.011	0.8316	
Lutjanus vittus	−10.5218 (0.1447)	2.9007 (0.0274)	223	11,186.525	0.9804	
Nemipterus furcosus	−10.9360 (0.1538)	3.0150 (0.0297)	203	10,282.691	0.9805	
Nemipterus hexodon	−10.9499 (0.2803)	3.0188 (0.0550)	123	3,011.431	0.9604	
Pristipomoides multidens	−10.3481 (0.1032)	2.9054 (0.0179)	125	26,357.314	0.9952	
Pristipomoides typus	−10.3289 (0.1707)	2.8902 (0.0308)	33	8,794.451	0.9961	
Psenopsis humerosa	−10.6433 (0.3927)	3.0174 (0.0780)	115	1,495.187	0.9280	
Saurida micropectoralis	−11.6679 (0.4003)	3.0307 (0.0726)	261	1,744.792	0.8694	

[1] See Table 1 for common names.

Table 3

Estimates of mean and asymptotic standard error (ASE) of allometric parameters obtained for mixed sexes, males, and females of each of 14 species of groundfish, caught in northern Australian waters during 20 October to 16 December 1990 by fitting Equations 4 and 5 with $V[Y|X_3] = \sigma_2^2 X_3^2$ excluding the model error term (σ_e^2).

	Mixed		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.4010 (0.0624)	3.0386 (0.0107)	0.015684 (0.000536)
Lethrinus fraenatus	−11.0788 (0.2791)	3.0450 (0.0480)	0.011364 (0.001120)
Lethrinus lentjan	−10.8528 (0.1295)	3.0022 (0.0231)	0.011431 (0.000427)
Lutjanus erythropterus	−10.2207 (0.2246)	2.8559 (0.0371)	0.011478 (0.000598)
Lutjanus malabaricus	−10.4315 (0.0455)	2.8858 (0.0079)	0.015562 (0.000445)
Lutjanus sebae	−10.7324 (0.0705)	2.9885 (0.0124)	0.013522 (0.000691)
Lutjanus timorensis	−10.3142 (0.4613)	2.9015 (0.0766)	0.010599 (0.001097)
Lutjanus vittus	−10.5948 (0.0968)	2.9132 (0.0186)	0.012502 (0.000405)
Nemipterus furcosus	−10.3566 (0.1275)	2.8986 (0.0252)	0.028576 (0.000918)
Nemipterus hexodon	−10.8451 (0.1281)	3.0006 (0.0257)	0.021340 (0.000683)
Pristipomoides multidens	−10.4311 (0.0626)	2.9196 (0.0111)	0.012057 (0.000483)
Pristipomoides typus	−10.6917 (0.0692)	2.9547 (0.0134)	0.012299 (0.000737)
Psenopsis humerosa	−11.8293 (0.2619)	3.2521 (0.0518)	0.015465 (0.000673)
Saurida micropectoralis	−12.3549 (0.1919)	3.1555 (0.0346)	0.017171 (0.000567)
	Female		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.4694 (0.1271)	3.0499 (0.0214)	0.016512 (0.000844)
Lethrinus fraenatus	−10.8822 (0.4288)	3.0111 (0.0747)	0.011972 (0.001450)
Lethrinus lentjan	−10.9932 (0.1843)	3.0276 (0.0331)	0.011992 (0.000515)
Lutjanus erythropterus	−11.1343 (0.3913)	3.0106 (0.0646)	0.009438 (0.000718)
Lutjanus malabaricus	−10.6957 (0.1742)	2.9293 (0.0284)	0.015106 (0.000754)
Lutjanus sebae	−10.9216 (0.1938)	3.0211 (0.0328)	0.013024 (0.000956)
Lutjanus timorensis	−8.5443 (1.5702)	2.6085 (0.2606)	0.011468 (0.001567)
Lutjanus vittus	−10.4305 (0.1808)	2.8802 (0.0348)	0.012749 (0.000602)
Nemipterus furcosus	−8.0532 (0.2559)	2.4435 (0.0506)	0.030733 (0.001396)
Nemipterus hexodon	−10.4947 (0.1627)	2.9332 (0.0328)	0.017758 (0.000753)
Pristipomoides multidens	−10.4486 (0.1296)	2.9225 (0.0224)	0.012449 (0.000864)
Pristipomoides typus	−10.3916 (0.1853)	2.8998 (0.0333)	0.011512 (0.001461)
Psenopsis humerosa	−12.0680 (0.5276)	3.2992 (0.1032)	0.015033 (0.001037)
Saurida micropectoralis	−12.4710 (0.3370)	3.1768 (0.0598)	0.017557 (0.000955)
	Male		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.7895 (0.1296)	3.1023 (0.0214)	0.012092 (0.000760)
Lethrinus fraenatus	−11.5461 (0.4630)	3.1229 (0.0776)	0.009625 (0.001619)
Lethrinus lentjan	−11.1988 (0.3127)	3.0609 (0.0541)	0.009055 (0.000704)
Lutjanus erythropterus	−9.9036 (0.2774)	2.8003 (0.0458)	0.011754 (0.000834)
Lutjanus malabaricus	−10.5854 (0.1203)	2.9120 (0.0199)	0.014870 (0.000728)
Lutjanus sebae	−11.5462 (0.2006)	3.1212 (0.0334)	0.009834 (0.000989)
Lutjanus timorensis	−9.4896 (1.7559)	2.7646 (0.2898)	0.008735 (0.001411)
Lutjanus vittus	−10.5171 (0.1433)	2.8998 (0.0272)	0.012371 (0.000566)
Nemipterus furcosus	−10.9048 (0.1524)	3.0089 (0.0295)	0.014279 (0.000690)
Nemipterus hexodon	−10.9325 (0.2732)	3.0153 (0.0538)	0.023605 (0.001481)
Pristipomoides multidens	−10.3460 (0.1004)	2.9051 (0.0175)	0.011230 (0.000680)
Pristipomoides typus	−10.3560 (0.1709)	2.8951 (0.0311)	0.010902 (0.001254)
Psenopsis humerosa	−10.6920 (0.3878)	3.0271 (0.0771)	0.014853 (0.000951)
Saurida micropectoralis	−11.6947 (0.3976)	3.0356 (0.0721)	0.016898 (0.000725)

[1] See Table 1 for common names.

donia (Kulbicki et al., 1993), systematic data are lacking from northern Australian waters. Because our data covered relatively large size ranges of each of the 14 species of fish concerned, our estimates of allometric parameters and associated relationships will improve stock assessments of major groundfish in northern Australian waters.

Acknowledgments

We wish to thank J. Robinson of the School of Mathematics and Statistics of the University of Sydney for his valuable suggestion of the model, R. C. Buckworth and I. Knuckey, both of our Fisheries Division, for their useful comments on the manuscript, and A. Coleman and J. Lloyd also of our Fisheries Division for their assistance in acquiring the weight at length data. This project was funded partly by the Australian Fisheries Research and Development Corporation (90/15) and the former Australian Fisheries Service.

Literature Cited

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, Jr., G. R. Smith and R. E. Strauss.
1985. Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes. Special Publication 15, The Academy of Natural Sciences of Philadelphia, 277 p.

Caillouet, C. W., Jr.
1993. On comparing groups of fishes based on length-weight relationships. NAGA, The ICLARM Quarterly 16:30–31.

Calder, W. A.
1984. Size, function, and life history. Harvard Univ. Press, Cambridge, MA, 431 p.

Kulbicki, M., G. Mou Tham, P. Thollot, and L. Wantiez.
1993. Length-weight relationships of fish from the lagoon of New Caledonia. NAGA, The ICLARM Quarterly 16:26–30.

Mosimann, J. E., and F. C. James.
1979. New statistical methods for allometry with application to Florida red-winged blackbirds. Evolution 33:444–459.

Peters, R. E.
1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge, 329 p.

Pienaar, L. V., and W. E. Ricker.
1968. Estimating mean weight from length statistics. J. Fish. Res. Board Can. 25:2743–2747.

Reiss, M. J.
1989. The allometry of growth and reproduction. Cambridge Univ. Press, Cambridge, England, 182 p.

Saenger, R. A.
1989. Bivariate normal swimbladder size allometry models and allometric exponents for 38 mesopelagic swimbladdered fish species commonly found in the North Sargasso Sea. Can. J. Fish. Aquat. Sci. 46:1986–2002.

SAS Institute, Inc.
1985. SAS user's guide, Version 5. SAS Institute, Cary, NC, 956 p.

Schmidt-Nielsen, K.
1984. Scaling: why is animal size so important? Cambridge Univ. Press, Cambridge, 241 p.

Seim, E., and B. Saether
1983. On rethinking allometry: which regression model to use? J. Theor. Biol. 104:161–168.

Shoesmith, E.
1990. A comparison of methods for estimating mean fecundity. J. Fish. Biol. 36:73–84.

Showers, P. A. T.
1993. Length-weight relationships of five species of the family Sparidae in the Gulf of New Guinea. NAGA, The ICLARM Quarterly 16:32–33.

Wilkinson, L.
1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, IL, 638 p.

Superintendent of Documents **Subscriptions** Order Form

Order Processing Code:
* 5178

☐ **YES,** enter my subscription as follows:

Charge your order. It's Easy! MasterCard VISA

To fax your orders (202) 512–2233

____ subscriptions to **FISHERY BULLETIN (FB)** for $27.00 per year ($33.75 foreign).

The total cost of my order is $_____. Price includes regular domestic postage and handling and is subject to change.

_____
(Company or Personal Name) (Please type or print)

_____
(Additional address/attention line)

_____
(Street address)

_____
(City, State, ZIP Code)

_____
(Daytime phone including area code)

_____
(Purchase Order No.)

May we make your name/address available to other mailers? YES ☐ NO ☐

Please Choose Method of Payment:

☐ Check Payable to the Superintendent of Documents

☐ GPO Deposit Account ☐☐☐☐☐☐ – ☐

☐ VISA or MasterCard Account

☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐

☐☐☐☐ (Credit card expiration date)

Thank you for your order!

_____
(Authorizing Signature) 11/91

Mail To: New Orders, Superintendent of Documents
P.O. Box 371954, Pittsburgh, PA 15250–7954

Fishery Bulletin
Guide for Contributors

Preparation

Title page should include authors' full names and mailing addresses and the senior author's telephone and FAX number.

Abstract should not exceed one double-spaced typed page. It should state the main scope of the research but emphasize its conclusions and relevant findings. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely.

Text must be typed double-spaced throughout. A brief introduction should portray the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods, Results, Discussion** (or **Conclusions**), and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e. there can be no subdivision without at least two items). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the *U.S. Government Printing Office Style Manual* (1984 ed.) and the *CBE Style Manual* (5th ed.) for editorial style, and the most current issue of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States and Canada* for fish nomenclature. Dates should be written as follows: 11 November 1991. Measurements should be expressed in metric units, e.g., metric tons as (t); if other units of measurement are used, please make this fact explicit to the reader. The numeral one (1) should be typed as a one, not as a lower-case el (l).

Text footnotes should be numbered with Arabic numerals and typed on a separate sheet of paper. Footnote all personal communications, unpublished data, and unpublished manuscripts with full address of the communicator or author, or, as in the case of unpublished data, where the data are on file. Authors are advised to avoid references to nonstandard (gray) literature, such as internal, project, processed, or administrative reports, wherever possible. Where these references are used, please include whether they are available from NTIS (National Technical Information Service) or from some other public depository.

Literature cited comprises published works and those accepted for publication in peer-reviewed literature (in press). Follow the name and year system for citation format. In the text, cite Smith and Jones (1977) or (Smith and Jones, 1977). If there is a sequence of citations, list chronologically: Smith, 1932; Green, 1947; Smith and Jones, 1985. Abbreviations of serials should conform to abbreviations given in *Serial Sources for the BIOSIS Previews Database.*. Authors are responsible for the accuracy and completeness of all citations.

Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own. All unusual symbols must be explained in the table heading. Other incidental comments may be footnoted with italic numerals. Use asterisks for probability in statistical data. Because tables are typeset, they need only be submitted typed and formatted, with double-spaced legends. Zeros should precede all decimal points for values less than one.

Figures include line illustrations and photographs (or slides) and must be cited in numerical order in the text. Unless photographs are submitted on glossy paper with good contrast, we cannot guarantee a good final printed copy. Figures are to be labeled with author's name and number of figure. Use Times Roman font (upper and lowercase letters) to label within figures. Avoid vertical lettering except for *y*-axis labels. Zeros should precede all decimal points for values less than one. Figures may be submitted as computer software files (along with laser-printed copies), as photomechanical transfers (PMTs), or as high quality photographic prints. Send only xerox copies of figures to the Scientific Editor; original figures will be requested later when the manuscript has been accepted for publication. Figure legends should explain all symbols and abbreviations and should be double-spaced on a separate page at the end of the manuscript.

Copyright law does not cover government publications; they fall within the public domain. If an author reproduces any part of a government publication in his work, reference to source is considered correct form.

Submission

Send printed copies (original and two copies) to the Scientific Editor:

Dr. Ronald Hardy, Scientific Editor
Northwest Fisheries Science Center, F/NWC3
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112-2097

Once the manuscript has been accepted for publication, you will be asked to submit a software copy of your manuscript to the Managing Editor. The software copy should be submitted in *WordPerfect* text format (or in standard ASCII text format if *WordPerfect* is unavailable) and should be placed on a 5.25-inch or 3.5-inch disk that is double-sided, double or high density, and that is compatible with either DOS or Apple Macintosh systems.

Copies of published articles and notes are available free of charge to the senior author (50 copies) and to his or her laboratory (50 copies). Additional copies may be purchased in lots of 100 when the author receives page proofs.